Scientific papers of William Bateson

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SCIENTIFIC PAPERS
OF
WILLIAM BATESON

IN TWO VOLUMES
VOLUME I

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OF
WILLIAM BATESON

EDITED BY

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VOLUME I

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PREFACE

WHEN the Syndics of the University Press decided to issue a collected edition of Bateson's scientific papers in two volumes and invited me to edit them, it became necessary to decide what should and what should not be included within the limits proposed. For this reason a few remarks seem called for on the scope and plan of the present collection.

It should be at once stated that none of those writings are included in which Bateson appealed to an audience wider than the purely scientific one. These have already been collected and published elsewhere[1]. Apart from them, however, the present volumes bring together practically all Bateson's contributions to scientific journals, with the exception of the papers on the structure and development of *Balanoglossus* published in the *Quarterly Journal of Microscopical Science*, and of the lengthy series of Reports to the Evolution Committee of the Royal Society, 1902–1907. Important as these last are, their omission is less serious in that they are still to be procured from the Royal Society. Fortunately, however, each Report contains a summary of the facts recorded and of their bearing on the progress of genetical science. These summaries are reprinted in the present collection. On the other hand, I have included portions from two of his earlier books which have long been out of print and are difficult to obtain. Of these one is the famous Introduction to the *Materials for the Study of Variation*, and the other, taken from *Mendel's Principles of Heredity—a Defence*, is the earliest reasoned statement of Mendel's work in English.

The arrangement of the papers is on the whole chronological, but I have not hesitated to disturb strict sequence in order to bring together two or more papers relating to the same matter.

As a whole the papers fall into two well-marked groups—an earlier one dealing mainly with problems of Variation, and a later one concerned chiefly with Heredity. Since the two groups are of approximately the same size it has been possible to keep them in separate volumes with little disturbance of chronological order. Each volume will contain its own index, and a full bibliography will be found at the end of the second one. Lastly, with the exception of a few obvious slips or misprints, the papers are as originally published,

[1] *William Bateson, F.R.S., Naturalist, His Essays and Addresses* (Cambridge University Press), 1928.

save for such small textual alterations as were found to have been made by the author in his own copies.

Thanks are due to the following Societies for permission to reprint papers which have appeared in their journals: the Cambridge Philosophical Society; the Entomological Society of London; the Linnean Society of London; the Marine Biological Society of the United Kingdom; the Royal Society; the Royal Horticultural Society, and the Zoological Society of London; also to the Editors and Publishers of *Brain*, *Biometrika*, *The Entomologist's Record*, *Nature* and *The Quarterly Journal of Microscopical Science*.

R. C. PUNNETT

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THE ANCESTRY OF THE CHORDATA

[*Quart. Journ. Micr. Sci.* XXVI, 1886]

PREFACE

In view of the facts relating to the structure of the *Enteropneusta* which form the subject of the accompanying paper and of those which have preceded it, it seemed necessary to attempt some analysis of their import and bearing upon morphological problems, and especially upon the vexed question of the ancestry of the Chordata.

But at the outset it was impossible to attempt such an analysis without first clearing the way by a discussion of the morphologic meaning of Segmentation. Since the Enteropneusta are essentially "unsegmented" animals and the Vertebrata are "segmented," this preliminary discussion was necessary. Moreover, having shown reason for not accepting the view that the vertebrate segmentation was of such a kind as to necessitate the existence of a series of segmented ancestors to account for it, it became also necessary to treat the whole question of the origin of segmentations of this class upon a wider basis. This must be the apology for the introduction into this paper of some matter and speculation not otherwise immediately relevant to the subject.

The decision that it would be profitable to analyse the bearing of the new fact in the light of modern methods of morphological criticism, does not in any way prejudge the question as to the possible or even probable error in these methods.

Of late the attempt to arrange genealogical trees involving hypothetical groups has come to be the subject of some ridicule, perhaps deserved. But since this is what modern morphological criticism in great measure aims at doing, it cannot be altogether profitless to follow this method to its logical conclusions.

That the results of such criticism must be highly speculative, and often liable to grave error, is evident.

PART I

The Segmentation of Amphioxus and the Vertebrata, compared with that of the Annelids

From the time when the theory of descent in some form or other became generally accepted amongst zoologists, the question of the pedigree of the Vertebrates has been the subject of much speculation and controversy. The amount of attention which has been bestowed on this question has perhaps been greater than is warranted by the actual importance of the problem considered as a contribution to general biology; but when it is borne in mind that the question is that of the history of the human race, the fascination which has been found in it is not surprising.

Beyond, however, this more sentimental side, there is another source of special interest to be found within the terms of the problem itself; namely, that which is afforded by the obscurity of the solution; for when the relation of any one group to the rest of the animal kingdom is sought, in most cases there are some cardinal features of anatomy common to it and to some other group, which appear to point to some affinity between them. For example, the structure of the Tracheata at once suggests Crustacean affinities, while there is a strong apparent resemblance between the whole Arthropoda and the Annelids. Even a group so isolated as the Mollusca has points of obvious harmony with other groups as soon as the characters of the Trochosphere are known, and similarly with most other groups. Each and all of these "obvious" resemblances may be illusory, but still they furnish something which, temporarily, is satisfying, and at least provides a point of departure for criticism. But in the case of the Chordata there are none of these common features. The three characters which unite them, the notochord, the gill-slits, and the relations of the nervous system, are limiting and exclusive, and without parallel in any forms outside the Chordate group. So strongly has this fact been felt by many of those morphologists who have already dealt with the pedigree of the group, that they have practically abandoned the attempt to find homologies for these features among the Invertebrates; for it is impossible to take seriously such suggestions as, for example, that the notochord may be compared to, generally, the sacs of the Capitellidæ, the "siphons" of any of various Invertebrates, the "giant-fibres" of Earthworms, or the crystalline style of Anodon. Each of these structures has been in turn suggested,

together with many others, as offering something with which to compare the notochord. In the same way Semper argues that the vertebrate gill-slits have an obvious similarity to certain pores which he has found in the heads of certain Oligochæta (Nais), while other authors see a striking resemblance between them and the Chætopod segmental organ, and so on.

In seeking, then, for the proximate ancestors of Chordata, the Chordate features have been disregarded, and another character of the vertebrate animal has been selected as offering a more probable basis of operations. The character which has in this way been chosen as the point of departure is that of *metameric segmentation*. By thus setting aside the questions arising out of the notochord, etc., and speculating upon the segmentation of the body, the conclusion is soon reached that some Annelid was the immediate ancestor sought.

This view has found its chief exponents in Dohrn and Semper, and has been generally supported by Haeckel and by most of the popular exponents of evolution.

It would be unprofitable to recapitulate here the numerous morphological difficulties as to the primitive mouth, etc., which arise if this theory be received. Many objections of this kind have been raised and have been variously replied to, and in this condition the matter rests. By those who support it, it is assumed that the common feature of segmentation is so binding and unique a property as to suffice to link together groups whose morphology is otherwise widely different.

In the following pages it is proposed to examine the propriety of employing the character of metameric segmentation as one of first importance in forming a phylogeny of this kind. And before referring to the evidence derived from the fact that the three characteristic features of Chordata are found in Tunicata and Enteropneusta, which are unsegmented forms, it will be best first to discuss the meaning of the phenomenon—"segmentation"—for if resolved into its elements it will be found to be by no means a peculiar feature of a few groups, but rather the full expression of a tendency which is almost universally present.

The term "metameric segmentation" has been used to describe several anatomical features, which reach their highest development in the Annelids, the Arthropods, and the Vertebrata. If an attempt be made to reduce this expression to its simplest terms it appears to mean, in the first place, that certain organs of the body are serially

repeated from before backwards, and in the second place that, in the case of the Vertebrates and Annelids at all events, the body cavity is at some period of life divided into a series of compartments, each of which is closed off from its neighbours. But when a more precise account of this phenomenon is required, and when it becomes necessary to particularise as to which of the various organs of the body is thus repeated, difficulty at once arises from the fact that this repetition is irregular, and even within narrow limits may vary considerably. In the case of many of the errant Polychæts all the mesoblastic organs, together with certain apparently serially homologous parts of the nervous and digestive systems, may recur for a seemingly indefinite number of times in one individual, or even the whole animal may be repeated in a chain, thus giving the highest expression to the phenomenon. On the other hand, as in Lumbricus, etc., one or more of the mesoblastic organs may not be repeated; while in both Oligochæts and Polychæts there is a marked tendency to a division of labour between and specialisation of structure of individual segments or even regions of segments in various parts of the body. It thus appears that even among Annelids alone the fact of segmentation is not a circumscribed idea, but may include several phenomena which clearly differ from each other in degree, and possibly are also unlike in kind. For while in the case of Nais, etc., this repetition is complete, and is thus used as an obvious and simple mode of reproduction, yet in other worms it appears only to be concerned in increasing the length of one individual without adding to the number. Now, if these two conditions are merely various expressions of the same phenomenon the question at once arises as to which is its more primitive manifestation. Was segmentation originally a *repetition of all the organs for purposes of reproduction*, which process has become subsequently commuted into mere *increase in bulk*, or is this *complete repetition* to be regarded as the *final term in a series* of which the first was *increase in bulk*? Segmentation, as we know it, may clearly be viewed from either of these two standpoints. With regard to the Annelids, many authors have held that the former is the correct one; the question whether this is so or not cannot be discussed here, but in the case of the Chordata examination will show that their segmentation is of the latter class, and is the result of a summation of repetitions; and, being so, it is by no means a unique condition, which can unite forms otherwise unlike, as Chordata and Annelids, but is rather a result of the common tendency

to repeat parts already present, which tendency occurs more or less in almost all animals. But before communicating the features of Chordate anatomy, which point to this as the mode of origin of the segmentation of the class, it will be best to establish the fact that repetitions of this sort are common, and to examine the comparative evidence as to the manner in which they occur. It will then be seen that segmentations on the plan found in the Vertebrates are really extremely common, and appear to arise suddenly and in forms nearly allied to those in which they are not found.

Firstly, among the ciliated Platyhelminths a striking case is offered by *Gunda segmentata*, in which, as described by Lang, the diverticula of the gut, the testes, the yolk-glands, the tubules of the excretory organs, the transverse commissures, and the nerve-cord, are all regularly and synchronously repeated. Now, this case stands alone merely in the completeness of the repetition. All through the Turbellaria are to be found many instances of animals with great numbers of gut diverticula, with testes and yolk-glands scattered all over the body, with branched excretory systems, with anastomosing nervous networks, etc. Not only this, but instances are common in which some of these structures are repeated regularly, and others irregularly or not at all, as, for example, *Polycelis pallida* (Quatrefages), in which the ovaries are scattered and the testes are not, while the reversed condition is more frequent. It becomes probable that the repetitions of these organs did not phylogenetically occur simultaneously, but that repetition occurred at various times in each set of organs.

Again, among Nemertines in some species the saccules of the gut, the generative organs, and the circular blood-vessels are all repeated together and with great regularity, so as to produce a segmented whole. In other species these repetitions are not all formed or are more or less irregular, thus pointing to the fact that these repetitions have been acquired within the limits of the group. The development (*v.* especially Salensky, *Arch. de Biologie*, 1884) precludes at once the possibility of the ancestral form of Nemertines having been "segmented"; hence they, together with the Planarians, offer a type of a high degree of repetition being acquired within the limits of a group. Nor do these forms alone exhibit this feature as one peculiar to themselves, for there are few groups in which it is not found. Even among Mollusca, which are, perhaps, the most typically unsegmented of all forms, the Chitons may be instanced as examples showing that such complicated organs as shells may be repeated

within the limits of a small group. Moreover, in some Chitons bunches of calcareous setæ recur along the sides symmetrically to the scutes, producing an appearance not far removed from that of Arthropoda.

Another case is to be found among the Nudibranchs, in which the liver diverticula, which are peculiar to and characteristic of the group, not only recur in an obviously segmental manner, but may be arranged in several ways among the *Æolidæ*, being in some (as *Æolis papillosus*, *Æolis pulcher*, etc.) arranged in more or less regularly paired oblique rows, while in others (as *Dendronotus*) the liver cæca stand in paired, arborescent tufts, which are as definitely symmetrical in their repetition as any system of organs of a Vertebrate. In cases of this kind the regularity of these repetitions is obviously secondary, and all the other anatomical features show no trace of segmentation, which constitutes the great interest of cases of this kind from the point of view of the present argument.

The cases which have been so far mentioned have all been selected from *bilateral* animals, with a definite long axis in the direction of which they move. But the belief that repetitions of this sort are of constant occurrence as a factor in effecting modifications of general form, derives most remarkable support from the facts of the anatomy of radiate animals, especially of the Echinodermata. From embryonic evidence it may be regarded as almost certain that these animals are descended from a bilateral ancestor, and that their present form has been since acquired. Whenever this change took place it came to pass in some entirely unknown manner that the various organs came to be repeated round a central axis. However this may have been brought about, the fact remains that the number of such repetitions did not become a fixed and definite feature common to all the divisions of the group. For while the number *five* appears to be the limit of the repetition in the Echinoidea, Ophiuroidea, and Crinoidea, among the Asteroidea the arms of different *genera* have not the same number, nor do they necessarily occur in multiples of any number. For example, while in the divisions Asteridæ and Asterinidæ the prevailing number is again five, among the *Solasteridea* we find that the arms of *Solaster* may be thirteen or nine (as in *S. endeca*), in Heliaster from twenty-nine to forty. Not only is this true of living forms, but in the case of the fossil *Cystoidea* the plates were irregularly arranged and the perforations of the feet scattered, and in the *Blastoidea* the basal plates were *three*, though bearing *five radials* and interradials. All these facts point to a history of the occurrence of repetitions

among the various parts around a central axis. And perhaps more remarkable still is the extreme variability to be seen among individual members of living species.

For example, though *Asterias rubens* ordinarily possesses five arms specimens possessing six or seven arms are very common, while individuals with only four are not rare (the latter may possibly, however, arise from mutilation). In like manner specimens of *Brisinga coronata* are said to have from nine to twelve arms. Thus, in these cases the arms, with all the organs which they contain, may be spasmodically repeated as a mere individual variation.

All these animals move on the oral surface, and though, of course, the body may be regarded as arranged bilaterally round a longitudinal axis, yet in the locomotion of the animal this fact is not conspicuous (?). But in the Holothurians in which a long axis does again assume importance, though repetitions of this magnitude do not occur, yet there is a tendency for certain organs to arrange themselves in a series of longitudinal repetitions closely imitating segmentation. In this connection the *Elasipoda* (Holma Théel, *Challenger Monographs*), which crawl about on the "trivial" surface in the direction of the long axis, are of great interest. The body of these animals is long and flat, and its margins are produced into long processes, resembling parapodia, which are regularly arranged in pairs down the sides. The regularity of this arrangement is so great that some of the species figured by Théel might easily be thought at first glance to be segmented worms[1]. Thus, in animals whose long axis has been suppressed, it appears that repetition may arise of most of the organs of the body radially arranged; next, that not only the specific but also the individual number of these variations is liable to great variations, pointing to the fact that the power to repeat in this way is one which may be easily called into action producing great differences of form.

It may also be observed in this connection that similar casual repetitions are frequent in the case of the Gonozooids of *Hydromedusæ*, in which animals also they are radially arranged. As in the case of the Echinodermata this is shown by the great diversity in the

[1] In relation to this acquisition of the appearance of longitudinal repetition or segmentation by a radiate animal, an example of the inverse phenomenon may be given. Among the Operculate Cirripedes, though in the Balanidæ the six plates composing the "cone" are so placed as plainly to indicate the original long axis, yet in the Coronulidæ this feature becomes obliterated, and the plates are disposed in a *radially* symmetrical manner.

specific and individual number of those organs which are radially repeated. The latter may be seen, for example, in *Clavatella prolifera*. The Medusa of this animal creeps about on its tentacles, which are long and stiff, and which carry short suctorial processes on their oral faces which support the animal, giving it the appearance of an Ophiurid. The number of these tentacles and of the radial canals varies with age, from six to eight (Hincks). In the specimens which have come under my own observation in the undetached buds the number of these arms was five, while that of the free Medusa was generally six. The number of the organs in *Cladonema radiatum*, another creeping form, is also very variable, the number of oral lobes being five or seven, and that of the tentacles and canals eight or ten (Hincks).

The facts of Echinoderm and Cœlenterate anatomy above quoted, suffice to illustrate the statement that in animals whose organs are already radially repeated, variation consisting in the repetition of one or more of the peripheral organs is of common occurrence, and may affect large numbers of organs as in the case of the arms of Asteroidea, and may be of specific occurrence as in *Asterias rubens* and *Brisinga coronata*, or even ontogenetic as in Clavatella, etc.

All the instances of repetition of organs which have been so far selected, whether in the case of animals with a marked long axis or in the radiate forms, have been examples of the recurrence of parts or organs in some more or less definite relation to the axis of symmetry of the animals. These have been chosen especially as more markedly illustrating the possibility that the segmentation of some forms at all events may have been derived from the continual recurrence of this phenomenon until it became more or less regular and transmissible to the offspring as the definite course of development. But it must be remembered that repetitions of this kind are of an extreme type. The recurrence of whole sets of organs, as in the case of the arms of Asterias or the gastric pouches and generative organs of the Nemertines, must be regarded as the higher manifestations of this phenomenon, and consequently of more or less occasional occurrence. Since, however, it is in these cases that the nearest approach has been made to metameric segmentation as we now see it, they have necessarily been selected as of the first importance. But if repetitions of this magnitude are of rare occurrence, repetitions of smaller parts or organs are extremely common, if not universal.

There is hardly one of the larger or more organised types in which whole tracts of the body are not composed of almost precisely similar and "serially homologous" parts, which are of very variable number. The scales and fin-rays of fishes, the tufts of hair and markings on many caterpillars, the teeth of Vertebrata, the joints of the Arthropod appendages, or of the stems of a Crinoid, the ossifications in the ambulacra of the Echinodermata, and many others, suggest themselves at once.

Especially noticeable are the casual repetition of large complex structures, such as the mammary glands, and of exoskeletal organs, as the horns and dermal scutes of Vertebrates. The number of these is liable to great variations, not even being constant in the species. For example, certain deer and also certain sheep have specifically more horns than two; and in the case of Iceland sheep the horns may be three, four, or five (Youatt, *The Sheep*). By the nature of the case none of these repetitions can be atavistic; and it is interesting to notice how, just as it was shown that irregular repetitions of parts about the axes of symmetry of the body often take up regular secondary relations to them, recurring either in segmental pairs or in radial symmetry, so these minor repetitions take up regular relations (secondary in some cases, probably primitive in others) to the axes of the limb or part of the body in which they occur. Thus the ossifications in the Crinoid stem or the Starfish arm are so regularly related to the axis of the part that in the latter case they have suggested to Haeckel his extraordinary view of the phylogeny of the group, appearing to him precisely similar to the segmentation of a Chætopod. The case of the scales of fishes and the hairs and markings of caterpillars should perhaps have been more properly quoted in the former connection, as being an instance of irregular repetitions which have become definitely related to the symmetry, as in the case of the Sturgeon, and among caterpillars the Tussocks and the Spherigidæ. One very curious instance may be quoted of a series of repetitions which, though essentially arranged with reference to the axis of a limb, have yet a definite relation to the long axis of the body. This instance is that of the Vertebrate tail, which has often been adduced by opponents of the Annelid theory of Vertebrate descent. Now, the structures which repeat themselves in the Vertebrate tail with great variability of number, namely, the vertebræ with their neural and hæmal arches, the segmental vessels and nerves, etc., are precisely those structures upon whose repetition in

the trunk the view of the primitive character of the segmentation of the Vertebrata mainly depends.

In the foregoing pages the attempt has been made to show that greater or less repetition of various structures is one of the chief factors in the composition of animal forms, that these repetitions may be of greater or less extent, affecting single or many organs, and may be at first irregular, and finally culminate in regularity, and that even this regularity may afterwards vary so as to become a symmetry of a different order. It is further contended that between repetitions in these varying degrees it is impossible to draw any hard and fast distinction, for nothing more can be affirmed as yet about them than that they are repetitions. The reason for their appearance is as yet unknown, and the laws that control and modify them are utterly obscure. But in view of what has been adduced it is surely not too much to say that enough of their mode of working can be seen to enable us to realise that they are at least powerful enough to have produced anatomical features of high importance, and further that the metameric segmentation of the Vertebrata is distinctly of the kind which could be brought about by their operation. That in this case they have attained a degree of completeness far exceeding that which they elsewhere present must be admitted; but there is no evidence to show that this result differs in kind from that which occurs on a smaller and more restricted scale in almost all animals. Whether the repetitions which occur in the Annelids and Arthropoda are also the products of this force in a still higher degree cannot yet be certainly stated.

General Conclusions as to the Mode of Occurrence of Repetitions of Organs

In the present state of biological knowledge no guess can be hazarded as to the cause of the facts above quoted. The solution of the problem must be sought in a fuller knowledge of the laws of growth and variation, of which we are still ignorant. As yet only one or two features in these repetitions may be mentioned as possibly of importance, though even these can only be selected in the most tentative manner.

In this connection the first noticeable fact is that the structures repeated in the Triploblastica are very generally of *mesoblastic* origin, and that when other structures have become involved this would appear often to be a secondary occurrence. To such an extent

is this true that in a recent contribution to this subject (Caldwell, *Quart. Journ. Mic. Sci.* 1885), a suggestion has been made which proposes to give a simple physical explanation of all the phenomena of segmentation. Caldwell suggests that owing to the early acquisition of the long axis of the body and the consequent elongation of the blastopore, the mesoblast has become, so to speak, left behind in blocks, in consequence of the more rapid growth of the epiblast. That this extremely simple theory will not account for all cases of repetition is shown, firstly, by the fact that though the repeated structures are generally mesoblastic, yet they are not always so; secondly, that the mesoblast does not thus originally segment as a whole, but rather that separate organs repeat themselves separately, as has been already urged, especially in the case of the Turbellaria; and finally, these repetitions are by no means universally embryonic or even larval features, but their whole history rather points to their having very generally originated in the adult condition, and to the view that they have come to be thus earlier in development, the opposite of which is assumed by such a hypothesis as Caldwell's.

This belief that these repetitions have had their origin in variations which occurred in the first instance late in life is founded upon several considerations. Firstly, the cases in which the generative organs are repeated are very numerous; in fact, both organs or the testis, at all events, are repeated in nearly all the cases in which much repetition is found (in most Dendrocœles, Chætopods, Nemertines, Balanoglossus, Amphioxus), even if few other systems are repeated. In the case of these organs it is most likely that the repetition first arose in adult life, and, in fact, in most of them it does still so arise; that is to say, the masses of cells which are to form generative organs are not specially broken up at an early age. And in the second place, the original late origin of repetitions is likely from the fact that most of them still so arise; it is only in exceptional cases as that of the mesoblastic pouches of Vertebrata, Phoronis, Enteropneusta, and the horns of the water-vessel of Echinodermata, that some of the repetitions are presented early in the development.

Besides the probability that most repetitions occur in the first instance in adults, or, at least, in mature individuals, it may also be noted as a general feature of them that they are at first very similar to, if not identical with, each other. For on their first appearance in an individual they do not generally arise phylogenetically in the condition which may be supposed to have been that in which

the original organs of the same series first arose, but rather from the first they are found as fully differentiated copies of the other members of the series, and not as rudiments. For example, the horns and teeth of mammals, whose number varies greatly, are, in those forms which possess additional ones, not repeated as tubercles or as plates, but rather as fully developed horns, teeth, etc. Though this is not universally true it is yet sufficiently well marked a feature to be of great importance in estimating the probability of the recurrence of such a complicated organ as a vertebra with its correlated parts within narrow limits of race. But no less noticeable is the tendency towards a subsequent differentiation and division of function among members of a series of similar parts as soon as the series is formed or any new member is added to it. This is of course to be seen in the case of the tentacles of *Hydromedusæ*, the division of the *ambulacra* of Echinoderms into *bivium* and *trivium* culminating in the bilateral symmetry of Holothurians, differentiation between vertebræ, etc.

Beyond this little can be predicated of the mode of occurrence of repetition of parts. Nothing is attained by analysis of the known facts which can be felt to be in any way a basis from which to interpret them. This much alone is clear, that the meaning of cases of complex repetition will not be found in the search for an ancestral form, which, itself presenting this same character, may be twisted into a representation of its supposed descendant. Such forms there may be, but in finding them the real problem is not even resolved a single stage; for from whence was their repetition derived? The answer to this question can only come in a fuller understanding of the laws of growth and of variation which are as yet merely terms.

Preliminary Remarks on the Repetition of Organs of the Chordata

In the foregoing pages it has been attempted to show (1) that repetition of organs and sets of organs is of common occurrence among animals, and (2) that however far back a segmented ancestor of a segmented descendant may possibly be found, yet ultimately the form has still to be sought for in which these repetitions had their origin. Hence it follows that in no case must it be held *à priori* impossible that an unsegmented form showing no degeneration should be related to a segmented stock. But when inquiry is made in the special case of the Chordata as to the condition of the repetitions found among them, it will be seen that so far are they from suggesting

that their immediate ancestor of the group must have been segmented, that they even preclude this view. As will be shown, there is a history of the actual steps by which several of the organs (the nervous system, the axial skeleton, and the mesoblast) acquired their repetitions within the group, and certain other structures (the notochord, etc.) persist in an unsegmented form. So that instead of regarding a fully segmented form as their possible ancestor it is necessary to search for a form in which these particular sets of structures at least are not repeated.

For in the first place, taken generally, the development of a Vertebrate consists in the gradual appearance of repetitions, first of one organ and then of another, until at last a climax is reached. The mesoblast divides into blocks, paired peripheral nerves grow out, and segmented tubules arise in connection with the excretory ducts, but the mesoblastic plates were at first unbroken, the medullary plate continues without transverse divisions, though its peripheral organs may be repeated, and the excretory ducts are single tubes with single openings. That many of these structures roughly correspond with each other is no doubt true, but these correspondences are only partial, and, as will be shown in the sections on the nervous system and vertebral column, a history is preserved to us of the steps by which some, at least, of these repetitions have been attained and of stages in which these correspondences were still more irregular.

The attempt to find the ancestor of the Chordata resolves itself first into the question as to whether the Chordate features, viz. notochord, gill-slits, and nervous system of a particular type were first associated in a form which possessed repetitions in a high degree or not. Now, since the notochord is always unsegmented, it is *à priori* likely that it arose in an unsegmented form; for, having in view the early period of development at which it arises and the situation which it occupies in the body, and the fact that it is found in the dorsal wall of the gut, the sacculation of which is one of the commonest features in segmented forms, it could hardly have thus arisen without participation in such segmentation. On the hypothesis of Annelid descent the facts of the morphology of the notochord are inexplicable; for, seeing that no homologue of the notochord exists among Annelids, on the theory that Vertebrates are their descendants, the notochord must have arisen subsequently to that segmentation, to account for which the Annelid ancestor is postulated. If this were so the notochord, by every rule of phylogenetic interpretation, might be expected

to arise *late* in development, and to exhibit marked segmentation, instead of which it is almost the earliest organ formed, and is absolutely unsegmented.

Similarly from the first, the medullary plate is distinctly a single structure, and without suggestion of transverse division. Not until the peripheral nerves arise is any serial repetition to be found in it, and were it not for theoretical considerations it would not have been supposed that the nervous system of a two-day Chick was a segmented structure. Further, in Amphioxus and the Marsipobranchs the serial repetition, even of the peripheral nerves, is not regular and opposite, the further meaning of which facts will be discussed later.

Lastly, the gill-slits are by their nature repeated structures; but, seeing that nothing resembling them occurs outside the group[1], their origin and, *à fortiori*, their repetition has been acquired within it.

It becomes then probable, from preliminary examination of the morphology of the three typically Chordate features, that their first origin was not in a segmented form. There is also one other structure which certainly points in the direction of an unsegmented animal as the immediate ancestor of the Vertebrate. This structure is the liver. Now, the liver is essentially a unique structure in the body which is not repeated. On the Annelid theory of Vertebrate descent it would have to be supposed that the liver either arose as an enlargement of one of the segmental saccules of the gut, or by the coalescence of several. The evidence attainable on this point is distinctly against either of these possibilities; for the liver of all the Vertebrates, and especially of *Amphioxus*, is markedly and obviously a single structure, not formed by the coalescence of several, while its asymmetrical position and general appearance favour the view that it is a structure newly formed within the limits of the group, rather than a relic of a paired sacculation.

Having then disposed of the *à priori* objections to regarding an unsegmented form as a primitive member of the group, the attempt will be made to show that the *Enteropneusta* occupy this position. After this we will proceed to consider the light which this admission will give on the history of the steps by which the organs of the other Chordata acquired their present arrangement, and finally to determine the relation which the various forms included under this head bear to one another.

[1] For Semper's suggestion that the cœlomic pores on the heads of some Oligochæts are of the same nature cannot be seriously considered.

The Enteropneusta as Members of the Chordata

The general features of the anatomy of the *Enteropneusta* place them in a very isolated position. They are extremely like one another, but apparently very unlike any other group of animals. Before Tornaria was known to be a stage in their development they were assumed to be worms of some kind, but after Metschnikoff had succeeded in proving Tornaria to be the larva of a Balanoglossus this was felt as an impossible view of its affinities. Up to this time Tornaria had been regarded by Joh. Müller, who first described it (*Berl. Akad.* 1849, 1850), and by others who examined it as a varied form of Bipinnaria, which, indeed, it very closely resembles, differing only in the presence of eye-spots, and of a peri-anal ring of cilia; both of which structures are liable to great variation. When, then, Metschnikoff discovered its real destiny, it appeared at first sight necessary to suppose the Enteropneusta closely connected with the Echinodermata, and accordingly Metschnikoff (*Zool. Anz.* 1880) proposed to include them in a division *Bilateralia* under the Echinodermata, the remainder of the group forming a parallel division, *Radiata*. But this generalisation with regard to the group was made solely on the characters of the larva, and almost without reference to the structure of the adult, which, indeed, was little known. So certain, however, did the conclusion seem, that Metschnikoff was led to suppose that the gill-slits of Balanoglossus were mere amplifications of the water-vascular system of Echinoderms, which could hardly have been suggested had it not been felt that no other solution was possible. Since this time the anatomy of the adult has become more fully known, and another mode of development has been shown to occur, and from neither of these additional sets of facts can any confirmation of the Echinoderm theory be derived. Hence we must conclude that the characters of Tornaria are not to be looked to solely in attempting a solution of the problem.

In the development of *Balanoglossus Kowalevskii* the following important features occur: (1) the origin of the central nervous system is by longitudinal delamination from the skin in the dorsal middle line; (2) at the anterior end of the body a portion of hypoblast is constricted off on the dorsal side to form a supporting structure, *i.e.* a notochord; (3) the gill-slits are formed as regular fusions and perforations of the body wall and gut from before backwards. Hence the three features which alone distinguish Chordata from other

animals are present, and associated from an early period in development. Added to this the minor features of Chordate anatomy are also represented by (1) the origin of the mesoblast; (2) the remarkable asymmetry of the anterior parts; (3) the opercular fold; (4) the excretory funnels opening into the atrial cavity thus formed. From all these facts we may form a preliminary conclusion that the Enteropneusta bear some relation to the Chordata. We will now discuss what relation this is, and before doing so we must determine what relative importance is to be attributed to the two modes of development known to occur, the one largely embryonic the other pelagic.

In our present state of ignorance as to the mode of development of Tornaria and of the details of its later stages, it is difficult to compare these two modes, but the question as to which is to be regarded as primitive is probably a part of the larger question as to the comparative likelihood of the preservation of ancestral features in the free or in the protected developments. This question cannot be fully gone into here. No general answer has as yet been given to it, and since the balance of probability is very nearly divided between these two possibilities we may be right in assuming either of them to be correct. For the purposes of the following argument it will be assumed that, on the whole, development within an egg-shell, as involving a less complicated struggle with environmental forces, is less subject to variation than that in the open sea, and consequently is more likely to preserve ancestral features. Besides this, in the special case before us, the adult structure is practically conclusive against Echinoderm affinities, to which the pelagic development would point if regarded as primitive.

Assuming, then, that the development of *B. Kowalevskii* is more primitive than that involving a Tornaria stage, the following features are of great importance:

(1) The animal is ciliated and inhabits muddy sand.

(2) The præoral lobe is enormously developed.

(3) The notochord arises at the anterior end of the hypoblast and grows forwards.

(4) The origin of the central nervous system consists in the delamination of a solid cord of epiblast in the dorsal middle line of the middle third; this, by invagination of its two ends, is afterwards extended as a tube in both directions.

Other collections of nerve-fibre are afterwards deposited in various parts of the body, and finally a general network of nerve-fibre occurs

at the base of all the skin of the body, especially in the line of the gill-slits.

(5) The mouth originally faces *ventralwards*, but comes afterwards to open forwards, being *not a sucking* but a *digging* mouth.

(6) The gill-slits *for a long time are only one pair*, but subsequently are repeated in pairs, increasing in number with increase in the size of the body.

(7) The mesoblast arises as one unpaired pouch, followed by two pairs of pouches.

(8) The blood-system is entirely peculiar, consisting of an anterior heart and a dorsal and ventral vessel, and in *B. minutus* of two lateral vessels in the intestinal region. The two former are united by a plexus of trunks, which are placed under the skin and below the walls of the gut.

(9) The generative organs are repeated through a large part of the body; in the branchial region more or less following the repetition of the gill-slits.

(10) Of the excretory system little can be affirmed. The cells of the mesoblast appear to have a power of forming concretions, probably excretory, in their substance, and then throwing them into the body cavity. Here they form small aggregations. A large gland (containing a plexus of vessels), apparently performing their function, exists in the proboscis cavity attached to the end of the notochord.

From the proboscis cavity opens an asymmetrical ciliated pore, placed on the left side of the body, which in *B. Kupfferi* is stated to be *paired*.

From the middle body cavities open a pair of pores into the atrial cavity, which is partly enclosed by

(11) A rudimentary operculum.

Having these facts in view, and having set aside the preliminary objection that no high degree of segmentation is present in Balanoglossus, we may consider their bearing on theories as to the ancestry of the Chordata.

Previous Suggestions as to the Ancestry of the Chordata

Setting aside the possibility of Annelids having been genetically connected with the Chordata, the most notable alternative suggestion is that of Balfour, that the Nemertines might be thus regarded. This view has been supported and extended by Hubrecht. It has thus

been thought that the Chordate nervous system might have arisen by the longitudinal coalescence of two such cords as are present in Nemertines. But even the facts of other Chordate developments almost preclude the view that their nervous system is a double structure; the medullary plate of Amphioxus is distinctly single, and it is only in the medullary folds of higher and more complex forms that even an appearance of a double structure is produced, while no really double origin occurs. This being so, the mode of origin in Balanoglossus is practically conclusive against the theory of double origin. It is possible, and even likely, that Nemertines bear some distant relation to Chordata, as will be further discussed, but if this is so it can no longer be supposed that their nervous system is other than a special development within the group.

In most speculations as to the origin of Vertebrata, it is assumed that all the lower forms of Chordata are degenerate. The supporters of the Annelid theory especially are compelled to resort to this view severally in the case of the Ascidians, Amphioxus, and the Marsipobranchs. These, with the exception of the Enteropneusta, are the only forms which could have been used to throw light on the origin of the group, and they had to be expressly excluded because the suggestion as to the origin of the group had been made without regard to them. In the case of Amphioxus and the Marsipobranchs this theory of degeneracy will not bear examination.

It rests solely in the one case on the fact that Amphioxus has no developed sense organs and lives buried in the sand, and in the other on the semi-parasitic habit of life of the group. This degeneration is postulated to explain the lower degree of segmentation presented by these forms; and the fact remains that of all animals the worms which live most underground are the most segmented types which are known. Hence it cannot be assumed without ontogenetic evidence that degeneration in this direction has occurred. This ontogenetic evidence is entirely absent. Degeneration in this sense means a phylogenetic change of plan; and this change of plan should then leave a mark on the ontogeny, as occurs in Echiurus, etc.; but no event in the development of Amphioxus or of Lampreys points to any such change of plan. The development of these forms is a steady progress up to the point which the creatures finally reach, and in a case of this kind it is gratuitous to postulate degeneration in order to support a preconceived view of the morphology of the group. (Even in the Ascidians, though a well-marked change of this kind does

occur, yet it is not a deviation from a segmented to a less segmented form; for with the doubtful exception of Appendicularia, Ascidian tadpoles are quite without trace of segmentation.)

Again, no such evidence of a change of phylogenetic plan is found in the case of the Enteropneusta. Highly modified, no doubt, the adult animals are, but not degenerate. For these reasons the presumption of universal degeneracy on the part of all the lower Chordata will be dismissed, and an attempt made to systematise the facts as they are found.

The Habits of Life and Form of the Body of the Primitive Chordata

Habits of Life. The presence of gill-slits in all the Chordata may be taken as positive evidence that they arose in an aquatic habitat. Moreover, such a structure as the notochord cannot be conceived as having arisen in a fixed form. Hence they probably led a more or less free existence. This being so, they may either have been pelagic creatures, as the larvæ of Amphioxus, or may have crept in mud as the larvæ of *B. Kowalevskii*. Between these two possibilities there is little or no determining evidence. The only feature which seems likely to affect the question is the question as to the original point in the body at which the notochord first segregated itself from the gut. Unfortunately the evidence upon this point is divided. For if we suppose that the condition in Balanoglossus is primitive, and that notochord began as a rod in the dorsal wall of the anterior end of the hypoblast, then this origin would more or less point to a burrowing habit, the notochord functioning as a support for the head in this operation; but if the separation of the notochord in the middle of the body, as in Amphioxus, be held to be primitive, then this would point to a pelagic habit, the notochord serving as a fulcrum, from which the movements of the animal in swimming might be maintained. The absence of fins on the young Balanoglossus and on the young Amphioxus, though pelagic, appears to point slightly in favour of a burrowing habit, though no reliance can be placed on such slight negative features.

Primitive Mouth. There is one more point that does point in favour of a pelagic habit, namely, the fact that the anteriorly-directed *digging* mouth of both Balanoglossus and of Amphioxus is of secondary origin, being formed by a modification of a more primitive *ventrally directed* mouth.

Balfour, having the mouth of Lampreys and Tadpoles in view, held that the original Vertebrate mouth was *suctorial*. This the ventrally directed mouth *might* have been; but this fact does not interfere with the obvious possibility of a *digging* mouth having again intervened, from which such a mouth as that of the Lampreys could easily be derived.

Taking into consideration, then, the fact that in the most primitive forms the mouth is anteriorly directed, and that in the Lampreys it is also anteriorly directed, though of different function, we may tentatively suppose that though the mouth of the possibly original pelagic form was directed ventralwards, and was possibly suctorial, yet probably the mouth of the Marsipobranchs is derived from a digging ancestor, in which the mouth of the hypothetical pelagic form had come to be anteriorly directed in correlation with an acquired burrowing habit. In any case the facts of the Enteropneusta entirely confirm Balfour's view, that the Vertebrate jaws have been developed comparatively long afterwards.

The Skin. That the skin was originally ciliated there can be little doubt; also it is probable that at first plexuses of nerve-fibre were formed at the base of the ectoderm cells, such as may be seen in many if not all animals with ciliated skins of this type.

The Nervous System. The next question relates to the position and mode of the first formation of a differentiated nervous system. The evidence of Enteropneusta, Ascidians, and Amphioxus is united in showing that this first occurred in the dorsal middle line, and not by the coalescence of two lateral cords. The structure of the nervous system of Balanoglossus further shows us a stage in the process by which this nervous cord separated from the skin. By many authors it is supposed that this was accomplished in the first Chordata by an invagination, but the evidence of Balanoglossus is decidedly for the view that a process of delamination preceded this; and, indeed, this being the simple process, might naturally have been expected to have occurred first. *In Balanoglossus we see in the trunk the cord still in the skin, in the collar the cord delaminated, and at the ends of this cord the process of invagination commencing and leading to the presence of a lumen.* More than this, the mode of origin of the peripheral nerves is also seen; for those portions of nervous tissue which remain in the skin consist of fibres and a few cells. Into the nervous tissue thus composed run the tails of ectoderm cells, and out of them, on their inner sides, run many fibres into the subjacent mesoblastic

tissues. Now, the fibres entering this nerve-substance on its outer side are plainly *sensory*, or at all events *afferent*, and the fibres passing from it on its inner side are presumably *motor*, or at least *efferent*, seeing that they innervate the mesoblast.

It is clear, then, that on the separation from the skin of a cord thus composed the relations of the *efferent* fibres will not be changed, as they still remain in contact with the mesoblast. But, on the other hand, if this nerve-cord be entirely separated from the skin the supply of outer or *afferent* fibres is cut off from it, unless cords of epiblast remain to connect it with the skin. Applying this reasoning to the particular case of the separation of the *dorsal cord*, we see that the *afferent* fibres are entering it on its *dorsal* side, and that the *efferent* fibres are leaving it on its *ventral* side. If, then, the cord sinks in from the skin, the efferent fibres coming out on the *ventral* side to supply the muscles can still do so *without being gathered into cords*, remaining irregular as they do in Balanoglossus, but without dorsal cords connecting the main cord with the skin afferent impulses could only enter at the two ends which remain connected with the skin; hence I submit that it is probable that the three median cords in *Balanoglossus minutus*, etc., are to be regarded as the homologues of the *dorsal roots* of other Chordata. It is at once evident, from the physical exigencies of the case, that if the nervous system arose in this way the dorsal roots were from the *first sensory*, and that they did *not arise as differentiations* of roots of mixed function, as has often been supposed. If this is true, then, as the cord phylogenetically comes away from the skin before backwards the number of these dorsal cords will increase, until finally the cord lies connected all along the body with the skin by a series of median dorsal cords placed at intervals.

Now, returning to what is found in Balanoglossus, it is to be noted that, *first*, the cord separates from the skin as a solid rod connected at the two ends to the skin, and upon this condition invagination supervenes at the two ends, forming a *neural tube* in these regions. Let us follow the effect which an extension of this system of invagination along the cord will have upon the origin of the dorsal roots; for it is nearly certain that invagination in this case is secondary to delamination; the condition in Amphioxus, in which the medullary plate folds up after being enclosed, offering a stage of transition between the condition found in Balanoglossus and that of an Elasmobranch, for example. Since the invagination of a plate of tissue differs from the separation of a cord in the fact that it is not the central

line, but the two edges of the plate, which remain last in connection with the skin, it follows that, as the process of invagination phylogenetically arrives at the point of attachment of any one of these median dorsal roots, it must take up its new attachment at one of these two edges. It is thus not possible, supposing these views correct, that the dorsal roots could in the first instance have been paired, except on the hypothesis that as the process of invagination phylogenetically reached its point of attachment each dorsal root split into two; which is almost impossible, and which the condition of Amphioxus shows not to have occurred. The other alternatives would be (1) that all the dorsal roots should remain attached on one side to the cord; (2) that they should be attached irregularly to one side or the other; and lastly (3) that they should have been attached alternately to either side. From the nature of the case they could not be *opposite*. Now, the fact of their alternate arrangement in Amphioxus is almost a proof that the latter alternative was the one which occurred. (It may be observed that, as a physiological convenience, they probably supplied the two sides of the body alternately while yet attached in the middle line.) Thus the opposite origin of the dorsal roots is almost certainly secondary to an alternate arrangement. The fact that it is the foremost pairs which are opposite in Amphioxus seems to indicate that the process by which they became so occurred first anteriorly.

Let us now follow the history of the ventral roots as preserved to us. In Amphioxus the large nerves or dorsal roots supply the skin and certain sense organs placed among the muscular tissue (Rohon); but into each myotome, opposite each dorsal root, runs a bunch of loose nerve-fibres from the cord. This was stated by Rohon, but denied by Balfour. Improved methods of section cutting leave no doubt, however, that Rohon's observation was correct, and, indeed, these fibres may be easily seen. The presence of these bunches of fibres clearly gives us another step in the formation of the "segmented" nervous system. For in the simplest case, that of Balanoglossus, the muscles are not gathered into bunches, and the nerve-fibres likewise are irregular. In Amphioxus the muscles are already gathered into bundles, and the motor nerves follow them in this arrangement, but remain distinct from the dorsal roots. This therefore is a stage towards the gathering of the efferent fibres into a "*ventral root*"; in Bdellostoma this is already done, and though the dorsal roots are already approximately, though not quite opposite each

other, yet the ventral roots are not at the same level with them. Besides this, in Lampreys, the anterior and posterior roots are still not united into a common cord, though in Myxine they are thus arranged (Schneider and others).

In this the nervous systems of Balanoglossus, Amphioxus, Lampreys, and Myxine form a graduated series leading up to the condition found in higher Vertebrates, showing the evolution of the nervous system of Vertebrata from a solid cord in the skin to its condition as a closed tube whose walls give off a series of "segmental" nerves arising by roots of different functions.

[It will be seen that if this view be accepted it becomes very doubtful whether efforts to analyse the segmentation of the head can lead to any result, seeing that it almost follows that the head was differentiated as such before any complex metamerisation was present; and, indeed, were it not for theoretical considerations, it could hardly have been supposed that the head of a three-day chick, for example, was a highly segmented structure, seeing that the regular segmentation of the body conspicuously stops at its junction with the trunk. No doubt the cranial nerves may, by arbitrary divisions and combinations, be shaped into an arrangement which more or less simulates that which is supposed by some to have been present in the rest of the body, but little is gained by this exercise beyond the production of a false symmetry.]

The Axial Skeleton. The notochord of the Enteropneusta is so partially developed that it is not difficult to conceive that its presence in the middle third of the body may indicate a stage in its phylogenetic appearance. If while in this condition it was used as a fulcrum in swimming it seems further conceivable that if this organ grew backwards the condition of the Ascidian Tadpole's tail would be produced, though no stress can be laid on this view. As will be shown later on, it is likely for other reasons that the Ascidians separated themselves from the other Chordata before *Amphioxus*, or even the *Enteropneusta*.

By extending the separation of the notochord the condition of Amphioxus is reached. And next, the axial column of the Marsipobranchs shows us the notochord enclosed in a mesoblastic sheath as yet unsegmented. This process is foreshadowed by the presence of rings round the neural canal, placed between the nerves whose segmentation they follow. Finally, in the other Vertebrata the column itself is segmented, so that this is another instance of the appearance

of a typical segmentation in a system of a Vertebrate whose origin within the limits of the group is unmistakeably traceable.

The Myotomes. Intermediate conditions between the condition of the muscles of Balanoglossus and of Amphioxus are as yet unknown. I submit, however, that it is not impossible to conceive the formation of Myotomes by a simple mechanical process of gathering the muscular fibres into bundles. Their origin as Archenteric pouches may then be supposed to have originated from the fact that the ancestral mesoblast already arose thus, and when new bundles of muscles formed in the adult began to arise in the larva they arose in the same manner as the primitive mesoblast. That provision is made for the production of more mesoblast than that of the original fourteen pairs of pouches is shown by the presence of mesoblastic pole-cells in Amphioxus (Hatschek). In any case the existence of Balanoglossus proves that the notochord, gill-slits, and Chordate nervous system were present together before the myotomes were formed.

The Gill-slits. It is unfortunate that the facts of the Enteropneusta seem to throw no new light on the original meaning of gill-slits. That they do not do so tends, however, to show that probably gill-slits were from the first developed *as such*, and not as modifications of any previously existing organ, as has been sometimes held.

The folded skeletons of the gill-slits of Balanoglossus are remarkable in their resemblance to those of Amphioxus. Until the development of these latter is fully known no further comparison can be instituted. It is clear from their origin in Balanoglossus that no "myotomes" are obliterated between them (as has been suggested by some, with the hope of increasing the symmetry of the body), for plainly their repetition preceded that of the myotomes.

The Excretory System

Upon the origin of the excretory system of Vertebrata nothing can be affirmed from a study of Balanoglossus. The excretory systems of Vertebrata cannot be easily derivable from anything found in either Balanoglossus, Ascidians, or Amphioxus. The absence of any regular excretory system in these three forms may, perhaps, be correlated with the extraordinary development of their respiratory systems, which may possibly assist in this function. The one fact which is derivable from the morphology of Balanoglossus, Ascidians, and Amphioxus, is that it is nearly certain that the excretory system of other Chordata has been developed within the group.

The Pituitary Body and Proboscis Pore. Though no insistence is placed on the following suggestion, the plausibility of it is such that it cannot be omitted. On a previous occasion I have called attention to the fact that the pore which in Amphioxus leads into the left anterior body cavity is obviously homologous with the proboscis pore of Balanoglossus, which leads from the left horn of the anterior body cavity. In some species of Balanoglossus the opening of this pore is placed medianly, though opening into the left horn. Now, supposing the præoral lobe to atrophy, as in an Ascidian, so that the neural pore came to open into the buccal cavity, as occurs in these forms, it is clear that any pore placed dorsally between the neural pore and the mouth will then be directed ventrally, and open into the pharynx below the end of the nervous system. This is precisely the position occupied by the ciliated pit of an Ascidian, which leads into the gland described by Julin (*Arch. de Biol.*, 59). Hence with this pore and gland of an Ascidian the proboscis pore and gland of *Balanoglossus* may be compared. Next, supposing the end of the nervous system to dilate and form a brain which bends up by a cranial flexure it follows that on the atrophy of the proboscis (or rather before the proboscis was formed, this being peculiar to Enteropneusta) this pore will lie in the dorsal wall of the stomodæum, *i.e.* in the position of the pituitary body. More than this, any gland attached, as is the proboscis gland, to the end of the notochord, will, when this is flexed by the cranial flexure, be bent backwards with it to the place where its end comes to lie, *i.e.* above the pituitary involution. In this way the double structure of the pituitary body becomes intelligible. If these views are correct the pituitary body and its pore is to be regarded as the rudiment of a primitive excretory organ, which originally opened dorsally.

I have elsewhere shown the *primâ facie* resemblance of the anterior body cavity with its pore in Amphioxus to that of Balanoglossus, which in the Tornaria development is formed from the water-vessel (Spengel). This water-vessel is precisely similar to that of Echinoderms, being otherwise without parallel among animals.

The Affinities of the Chordata

Having thus examined the history of those organs which the morphology of *Balanoglossus* enables us to trace, let us consider the relations of Chordata (1) to other groups, (2) to each other.

Of the Echinodermata. Unlikely though it may seem, if any reliance can be placed on the characters of pelagic larvæ, we must assume some affinity between Echinodermata and Chordata, for Tornaria is not very like, but practically identical with, Bipinnaria. The case is like that of Mollusca, which may be supposed to be allied to Annelids, as is indicated by the trochosphere larva.

Of the Nemertines. So much has been said by previous writers as to the Chordate affinities of Nemertines that the subject cannot be omitted. The suggested homology of the nervous system has already been dismissed. Hubrecht has further suggested (1) that the notochord is homologous with the proboscis sheath of Nemertines, (2) that the cephalic pits are gill-slits, (3) that the proboscis is the pituitary body.

With regard to (1), what can be adduced from a study of Enteropneusta seems rather to be opposed to this view. If this were true, the notochord must have arisen in some such body as that of a Rhabdocœl, into the wall of the endoderm of which a præoral lobe could be invaginated, rather than as a hard thickening which is constricted off to form a lumen. Into the free end of such a structure it is impossible to conceive the invagination of a proboscis, which is what Hubrecht's suggestion seems to require. All that can be said is that the notochord of Balanoglossus suggests that it arose as a supporting structure and not as a modification of something else.

But supposing the larva in Stage G to represent a phylogenetic phase, several points of Nemertine anatomy can be derived from it. At this stage it has one pair of gill-slits, a short nerve-cord, one median anterior mesoblastic pouch, and two pairs of posterior pouches. Now, on the hypothesis of Hubrecht that the œsophageal pouches of Nemertines were the homologies of gill-slits, and supposing the proboscis invaginated and around its base a quantity of nerve-tissue deposited as in Balanoglossus, the proboscis would then have the same relation to the nerve-ring as that found in Nemertines. Hubrecht's view of the pituitary body falls if the alternative here given is accepted. Though the points of anatomical resemblance are not striking, yet when taken with the ciliated skin, the ventral mouth and position of the generative organs they form a basis for comparison.

If these resemblances were found to be real the nervous system of the Nemertines would have to be supposed to have arisen within

the limits of the group. As both animals possess a nerve-plexus in the skin this does not seem impossible. Also the excretory system lately described by Oudemans (*Quart. Journ. Mic. Sci.*, 1885), would have thus arisen as a specialisation of parts of the body cavity; since in Balanoglossus this function appears to be generally distributed over the body cavity, this also might be conceived.

Of the Tunicata. Next, since all the Chordata at some period of their development agree with the larva in Stage H, in possessing a dorsal nerve-cord more or less invaginated, one or more pairs of gill-slits and a notochord, let us pass on to Stage H, in which the notochord is forming at the anterior end of the gut. From such an animal as this the Ascidians may have been descended. For, as has been suggested by van Beneden and Julin (*Archives de Biologie*, 1885) it may be, that all the Ascidians have but a single pair of gill-slits; for that Appendicularia has only one pair is known; while in some genera the atrial cavity arises as an increase in the size of the pair of ciliated chambers by which the gill-slits open; and this increase may take place in the *hypoblastic* half of the chambers, or in the *epiblastic*; by the fusion of these two chambers the atrial chamber of these genera is formed. Van Beneden and Julin then suggest that the atrial pore is the actual opening of the two fused gill-slits, and that the rows of slits placing the pharynx in communication with the atrial chamber are to be regarded as secondary perforations. Whether this ingenious theory be adopted or not, the fact remains that Appendicularia is almost certainly a very primitive Tunicate, and also that the arrangement of the pharyngeal perforations of other Ascidians makes it unlikely that they are homologous with the gill-slits of higher forms.

The increase in size of the tail, which would speedily follow the first use of the backward directed notochord as a swimming organ is not difficult to understand. In connection with the increase of the tail the curvature of the gut would also be intelligible. From atrophy of the præoral lobe in correlation with the future sessile habit, coupled with increase of the lower lip to bear the suckers, the relations of the neural pore to the mouth would result. The gland of the præoral lobe would then, as before described, be placed below the nerve-ganglion and open into the pharynx.

It has been remarked by Seeliger (*Jen. Zeit.*, 1885) that the body of the Ascidian tadpole appears to consist of one head and two trunk segments. It may be observed that though the reasons for this belief

are not very obvious, this view, if correct, would coincide with the possibility of its descent from such a larva as Balanoglossus, Stage G, which also possesses one head and two trunk segments.

However the various points that have been raised in the preceding paragraph may be decided, it has seemed necessary to point out what conclusion with regard to the structure of Ascidians may be drawn from the development of Balanoglossus. That these are so meagre is to be regretted; the only tangible point appears to be the confirmatory evidence that it offers to the view that the atrial folds of Tunicata are not homologous with those of Amphioxus.

In this way only can the absence of mesoblastic repetitions in Tunicates be accounted for. Their development gives no support to the view that their ancestors possessed repetitions of this kind.

Of the Enteropneusta. That the Enteropneusta might possibly have had an ancestor in an animal possessing the structure of Stage H is of course shown by their ontogeny. They are derived from it chiefly by increase in size of the præoral lobe, change in direction of the mouth, growth of a rudimentary operculum, serial repetition of the gill-slits, and appearance of the generative organs also as a serial repetition. That any animal possessing a large præoral lobe should acquire a thick sheath of nervous tissue (especially when consisting of fibres for the most part) is easily understood. As shown in the foregoing pages, this mass of tissue is probably mainly composed of afferent fibres connecting the proboscis with the dorsal cord. As soon as the ventral nerve-cord arose as a concentration of nerve-tissue, this would naturally be followed by another circular concentration in the nervous sheath connecting the ventral cord with the central, invaginated, nervous system, also as an afferent mechanism.

In all probability the enormous increase in size of the larger species was a comparatively recently acquired feature, as also the peculiar odours which they emit; to this latter power it is possibly not too much to attribute the preservation of such a group.

Of the Cephalochorda. The relations of the Cephalochorda is the next subject for consideration.

The young Balanoglossus agrees with *Amphioxus, especially* in the following anatomical features:

(1) The digging mouth.

(2) The repetition and folding of the gill-slits.

(3) The repetition of the generative organs.

(4) The peculiar fate and remarkable asymmetry of the anterior mesoblastic pouch and proboscis pore.

(5) The presence of atrial folds.

(6) The *absence* of (*a*) any developed sense organs; (*b*) any excretory glands differentiated as such.

(7) In the presence of excretory tubes opening into the atrial cavity.

On the other hand it differs from it in

(1) The relative size of the præoral lobe.

(2) The degree of its mesoblastic repetition.

(3) The degree of the invagination of its nervous system and the extent of the neural tube.

(4) The extent and degree of isolation of its notochord.

(5) The extent of the atrial folds.

(6) The *absence* in *B. Kowalevskii* of any definite liver sacculi, and the presence in *B. minutus*, etc., of liver saccules differing from those of Amphioxus.

The points of resemblance taken together are so considerable as to suggest that they were possessed by a common ancestor of the Hemichordata and Cephalochorda. On the other hand, the points of difference are nearly all differences of *degree*, and (1), (2), (3), (4), (6) are points in which the Vertebrata agree with Amphioxus. In the case of (5), however, the Vertebrata more nearly agree with Balanoglossus.

Of the Vertebrata. The common ancestor, then, of the Cephalochorda and the Vertebrata may be presumed to have possessed the features of mesoblastic repetition, invaginated nerve-cord, and consequent extension of the neural tube, raised, so to speak, to the degree in which they are found in both those divisions. Also it may be believed that the præoral lobe had somewhat diminished and that the atrial folds were still small. The origin of such a liver as that of Amphioxus, as a specialisation of part of the wall of the digestive region of a young *B. Kowalevskii* is easy to imagine, for the histology of these two tissues is still almost identical. [The presence of peculiar liver saccules in *B. minutus*, etc., presents no difficulties, as their absence in the more primitive *B. Kowalevskii* shows that they have arisen within the limits of the group.] Animals possessing those features would answer nearly to the *Protochordata* of Balfour, though the structures now attributed to it are somewhat different.

The Protochordata thus constituted would then differ from the

Enteropneusta in the possession of a serially repeated mesoblast, in addition to serially repeated gill-slits, and possibly generative organs; also in the complete separation of the nervous system and notochord. The serial repetition of the gill-slits, the small operculum, etc., they must be presumed to have acquired from the ancestor common to them and the Enteropneusta.

In this way the connection of the Protovertebrata of Balfour with the other division becomes explicable on the new facts derived from the Enteropneusta.

The peculiar fact that so many of the features of the Enteropneusta differ from those of the Cephalochorda in *degree of expression* only is very remarkable, and suggests that their further evolution towards the Protochordate type proceeded by correlated variations affecting the several systems.

From the Protovertebrata thus constituted, which in all probability possessed an unsegmented mesoblastic sheath for the notochord and a brain, the Cyclostomata may be easily derived without the necessity of any hypothesis of great degeneration, which cannot be well supported.

Balfour has fully discussed the question of the origin of his hypothetical group of *Protognathostomata*, and upon the question of their immediate origin no new light can be thrown.

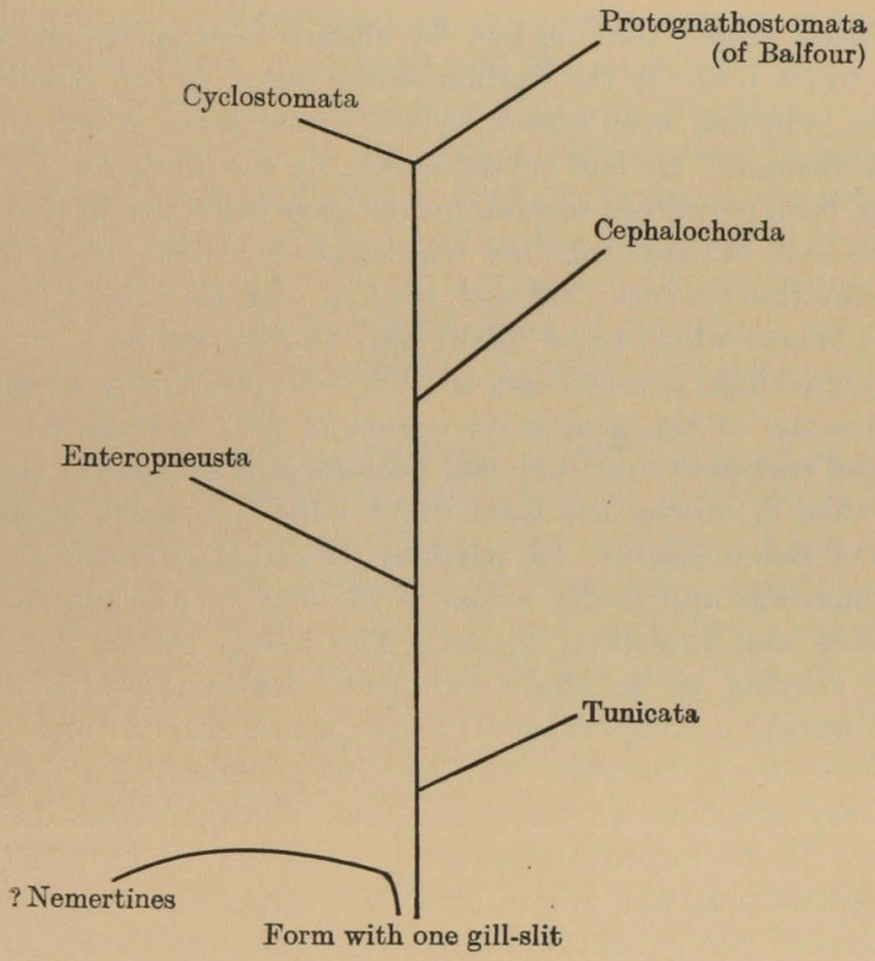
The above suggestions entail many difficulties. The chief of these is that they involve the hypothesis that the *rudiment of the notochord of the Archichordata* developed itself as a separate structure, once in the case of the Ascidians, and again in the case of the Protochordata. In the first case, owing to the atrophy of the præoral lobe and use of the tail in swimming, it came to lie in that organ, and in the second case extended through the whole length of the body. Also does this suggestion of the origin of the Tunicates involve the proposition that the rudiment of the dorsal nerve-cord extended itself twice along the body, once in the case of the Ascidians, and again in the case of the Protochordata. If this occurred there is no difficulty in supposing it to have been twice invaginated, this being a more or less common feature among nervous systems.

Another difficulty which affects all these suggestions arises from the epiblastic origin of the generative organs of *Enteropneusta*, in which they resemble the Echinoderms.

Though it is likely that many of the suggestions here made may be shown hereafter to be wrong, still it has seemed well, on the whole,

to analyse the facts as they stood, and to endeavour to reconstruct the past stages, whose existence is indicated by the lacunæ in the sequence of these facts, avoiding as far as possible a reliance upon phylogenetic changes of whose occurrence we have no evidence.

The foregoing views are, perhaps, more clearly expressed in the following table, which is not meant so much as a genealogical tree as to serve as an exhibition of the logical relation of the various forms, showing their points of divergence.



SUGGESTION THAT CERTAIN FOSSILS KNOWN AS *BILOBITES* MAY BE REGARDED AS CASTS OF *BALANOGLOSSUS*

[*Proc. Camb. Phil. Soc.* VI, 1888]

THE author stated that he had by chance seen specimens of these fossils, which occur in the Carboniferous series, in the Woodwardian Museum, and had been struck by the resemblance which they bore to *Enteropneusta*. He had subsequently, by the kindness of Professor Hughes, been permitted to examine his large collection of these forms, and had also brought together additional specimens from the place in Westmorland where Professor Hughes had discovered them.

The likeness which these fossils bear to *Balanoglossus*, in size and surface-markings, is very close, and they are practically a representation in stone of the generative region of that animal. The author suggested therefore that they had been formed as casts of the closely fitting tube of mucus and sand which envelopes parts of the larger species of *Balanoglossus*. He particularly called attention to a specimen which was apparently a cast of the body at the junction of the generative and intestinal regions. The fossils are of considerable length, varying up to about two feet. *Balanoglossus* is the only animal having a comparable structure which reaches such a length. Two species were exhibited of the fossil form which differed from each other very much as *B. salmoneus* (Giard) differs from *B. Robinii* (Giard). The texture of the sandstone was exactly that of the sand at the Glenans Islands where these two forms now occur. In some specimens, as pointed out by Professor Hughes, there were indications that the animals had lived immediately under the surface of the sand, which is not the case with existing forms.

The author wished to express his thanks to Professor Hughes for his assistance in this investigation.

ON SOME VARIATIONS OF *CARDIUM EDULE* APPARENTLY CORRELATED TO THE CONDITIONS OF LIFE

[*Phil. Trans.* B, CLXXX, 1889]

(With Plate I)

INTRODUCTION

THE following paper forms part of an investigation of the relation between the variations of animals and the conditions under which they live. It appears to me necessary that any investigation of this problem should be begun by the examination of cases in which difference in environment is known to exist, and that variations should then be sought for among the forms of life subjected to these conditions. If by this examination any variations can be shown to occur regularly with the change of conditions, or in any way in proportion to their intensity, it is so far evidence that there is a relation of cause and effect between them.

By thus first approaching the question from the point of view of the conditions, many difficulties are obviated which occur in any attempt which begins by ascertaining the variations in the animal, in the hope of afterwards finding an environmental change to which they may be traced. Such attempts to trace back variations to some environmental cause have often been made, and have, in general, been unsuccessful. In the case of species which have varied in isolated situations not apparently differing from each other, the failure to find points of environmental difference has been held to be evidence that the variations in question did not arise from such causes at all. This appears likely, and is probably true of the variations in question; but it must be borne in mind that the fact that no palpable difference can be found between the conditions in the several localities is no proof that they do not exist. While these differences in condition are usually evasive and hard to detect, it is best to begin to investigate their relation to variations in animals by selecting cases in which the change in conditions is unequivocal, and proceed from this starting-point to seek for correlated variation in the forms of life subjected to them.

It appears that a particularly favourable opportunity for investigating this question is offered by the fauna of isolated lakes of various composition and of different degrees of salinity, and the following

observations were made in accordance with this view. They are chiefly interesting owing to the great scarcity of any systematic observations of the relations between variation and the condition of life and to the rare occurrence of opportunities for investigating them.

While it has been held by some persons that the conditions of life are without definite effect in producing variations in animals, others, on the contrary, regard their production as an obvious consequence. The result of my investigations is to show that the whole relation between variation and conditions is much more complicated than it would be in accordance with either of these views; and that, while one animal may be profoundly and uniformly modified in every case by a certain change of conditions, yet these same changes produce no palpable effect on an allied animal of a different sort. For example, particulars will be given of the constant modification of *Cardium edule* consequent upon the drying up of the lakes in which they were, while *Dreissena polymorpha* and *Hydrobia ulvæ* do not appear to have been affected. It may be here remarked that the general variability of a form, as *Dreissena polymorpha*, does not appear to predispose it to assume a new form for a given change of condition.

In view of the fact that definite variations have been shown to be produced in *Cardium edule* by change in the composition of the water, it next becomes desirable to know to what extent these changes would be maintained if the conditions were altered back again to their original state. Upon this point I have no evidence; but that the animals would, if they lived and propagated, ultimately regain their former structure appears probable; for, since it can be shown that certain variations are constantly produced by water of certain constitution, it practically follows that the maintenance of these variations depends also on the same cause. It would, however, be of the greatest interest to ascertain the length of time and the number of generations necessary to effect these changes.

The specimens forming the subject of this paper were collected in the district of the Aral Sea and in Egypt.

In 1886 and 1887 I made a journey to some of the lakes of Western Central Asia, for the purpose of making observations on their fauna. As the waters of these lakes are of very various composition, being salt, alkaline, bitter, or fresh in differing degrees, I looked forward to an opportunity of investigating the question whether these diverse environmental conditions produce any correlated changes in the structure of the animals which are exposed to them. The collections

made with this object consist chiefly of Crustacea, of which an account will be published hereafter.

In the course of the journey thus undertaken, I visited the northern shores of the Aral Sea and the sandy region called Ḳara Ḳum, over a part of which, at least, the Aral Sea formerly extended, as is shown by the quantities of shells of the Aral Sea Cockle which are strewn on it. The area from which the Aral Sea has thus receded is not a level tract, but contains three considerable depressions, called respectively Shumish Kul, Jaksi Klich, and Jaman Klich. When the level of the sea was changed these three depressions remained, for a time, as isolated lakes, each containing a separate sample of the fauna of the sea living in it. The lakes gradually dried up, becoming salter and salter; and it is the object of the present paper to investigate the changes which befell the animals inhabiting them during this process.

General Account of the Desiccation of the Aral Sea

Before entering into a detailed account of these lakes, it may be well to describe briefly the present conditions of the Aral Sea itself, of which they once formed a part. As is well known, the Aral Sea is a closed basin, receiving the waters of two rivers only, the Syr Darya and the Amu Darya. In this respect, it resembles the Caspian Sea, which receives the Volga, Ural, and Emba rivers. It is universally supposed that these two seas were united at a comparatively recent period. The evidence for this belief is the statement that banks of shells of species now living in the Caspian Sea are found on the land lying between them. As the level of the Caspian Sea is now 84 feet below that of the Black Sea, and the level of the Aral Sea is 128 feet above that of the Black Sea, if it be supposed that the respective levels of the beds of these two seas were formerly the same as they are now, it follows that the Caspian Sea must, at the time of its connection with the Aral Sea, have been more than 200 feet deeper than it now is. On the other hand, the change in the levels of the two seas may have been due to subsidence of the bottom of the one, elevation of the other, or both. It is further supposed by many that the conjoined Aralo-Caspian Sea had a northward extension, probably on the east of the Ural range, thus connecting with the Arctic Ocean. One reason for this belief, amongst others, is the presence of a Seal in the Caspian Sea whose affinities are rather with *Phoca vitulina* of the Arctic Ocean than with *P. fœtida* of the Mediterranean. It has

also been supposed that this Aralo-Caspian Sea had an eastward extension as far as Lake Balkhash. The reason for this view is not easy to suggest, as none of the typical Aral fauna occur in Balkhash, nor are any deposits of Aralian shells found between the two waters. It may be added that Balkhash is bounded, both north and west, by very considerable hills, the Koi Djarlegan, etc.

Moreover, apart from the question as to the extent of the hypothetical Aralo-Caspian Sea, it has been suggested that the Aral Sea, at all events, has retired in recent times from some considerable area, and is continuing to recede thus. This statement, which occurs in several text-books, would appear to be only partially supported by the facts which came within my own observations. In the summer and autumn of 1886, I visited the whole north shore of the Aral Sea lying between Gulf Peroffsky and the mouth of the Syr Darya. From Togusken to Sary Cheganaḳ the shore is formed by high cliffs composed of horizontal beds of Eocene formation, containing fossils. Of these I collected some 130 species, which have been examined by Mr T. Roberts, of St John's College, and Mr Keeping, who state them to be of about the age of the London Clay and of the Bracklesham beds of England. In some places these cliffs rise from the water's edge, and in others recede from it, opening up considerable valleys which slope gradually down to the shore. In places where the cliffs do not abut on to the water there is generally a sandy beach, but occasionally, as at Ḳuḳturnaḳ, there is a steep bank of large shingle and pebbles. The shores of the Sary Cheganaḳ (Yellow Gulf), which forms the northern limit of the Aral Sea, are low lying and sandy. These sands extend northward and eastward for about 150 miles, constituting the Ḳara Ḳum (Black Sand). The southern edge of the Ḳara Ḳum is thus the northern shore of the Aral Sea, and it is generally assumed that it was covered by those waters at a comparatively recent period.

The waters of the Aral Sea oscillate greatly under the pressure of the wind, and this effect is especially seen when the wind is from the south for some days. The water is then driven in some hundreds of feet over the almost horizontal beach of the Sary Cheganaḳ.

The Mollusca which have been recorded as occurring in the Aral Sea are *Cardium edule, Adacna vitrea, Dreissena polymorpha, Neritina fluviatilis, Hydrobia ulvæ*. In addition to these I found *Hydrobia spica* in large quantities (this species is already known from the Caspian Sea) and also *Neritina* (? n. sp.).

The *Cardium* occurs in great numbers on all parts of the shore which I visited, and when the wind falls and the sea retires the shore is left covered with stranded cockles. The highest limit to which the flood thus induced ever reaches is in this way more or less clearly shown by the fresh shells and other *débris* left behind. Above the level of this fresh deposit the ground is always strewn with old shells, indicating the area covered in past times by the water. The coast of the south-west shore of the peninsula Ḳuḳturnaḳ is covered entirely with cockle shells, extending in a band nearly a mile wide. With the exception of those points in which the cliff rises from the water's edge, there is always a tract of shore on which shells are found. On the hypothesis that the Aral Sea formerly had a much greater depth than at present, it would be expected that shells would be thus found in position for a considerable height above the present level, but this is not the case. On the contrary, where the shores are more or less steep the shells are found in great quantities up to a certain level, about 15 feet above the water, and above this level they are never found. In places where the land slopes very gradually to the water level the horizontal extent of the shell-covered tract is very great, being as much as 15 miles in some places; but whenever the ground rises suddenly so as to reach a greater height than about 15 feet above the Aral Sea level no more shells are found. The fact that the shells cease abruptly at a definite horizon is true both in sandy parts of the coast and on the clayey tracts, and it is equally true of those deposits of shells which occur in the bottom of valleys opening to the sea which are now altogether dry, but which were formerly filled by the sea. Some of these deposits of shells reach inland four or five miles (*e.g.*, Meregen Sai), but always without any marked rising of the ground; where any elevation occurs the level at which the shells cease is always definite and striking.

The absence of shells above a definite level seems to suggest that the sea has never in recent times extended over parts above that level. There is nothing to suggest that any Aral Sea deposits, higher than this line of demarcation, have been denuded. For, had denudation been the cause of the absence of Aral shells above this line, it would be expected that the shells would *gradually* disappear on a line travelling up from the sea, and that they would disappear at different levels in different places, which is not the case. If, therefore, the Aral Sea did ever extend over a greater tract of country than that which would be covered by it if it rose about 15 feet above its present

level, it can only be supposed that such a condition occurred in the remote past, and not that it has gradually diminished to its present size from a much greater extent, as has been often suggested. Moreover, if the Aral Sea had recently retired from a greatly extended area, it must have covered the Ḳara Ḳum entirely, extending to Lake Tschalkar, which is marked on the Russian maps as a lake about 40 miles long and 25 miles broad, forming the termination of the great valleys of the Irghiz and Turgai streams. In the belief that such a connection might have formerly existed between Lake Tschalkar and the Sea of Aral, I travelled down the Irghiz river as far as the lake. I found it to be a vast sheet of salt mud, which becomes dry in summer in most places. The joint stream of the Irghiz and Turgai never reaches the main part of the lake, becoming lost in reedy morasses of nearly fresh water at the western end. The lake was so dry that my camels crossed the west end of it in the beginning of August. Its northern shore is bounded by a range of hills which rise about 600 to 800 feet from the lake. The southern front, which faces towards the lake, is nearly vertical, and is cut in places by ravines. These hills are composed of horizontal beds containing Eocene fossils, similar to those which were found in the hills on the north-west of the Aral Sea. Above these beds was a deposit of horizontally stratified sand about 80 feet thick.

In no case, either in the ravines, or among the hills, or on the shores of the lake, or in the *débris* thrown up at the mouths of the wells, were any shells found other than those of the fossiliferous beds. There was no trace of the previous presence of the Aral Sea. The ground did not differ in any way from considerable low-lying tracts near the Aral Sea, which remain covered with cockles; and, had the sea recently been in Lake Tschalkar, these shells could not have failed to be found in quantity. Also in the Ḳara Ḳum, excepting the above-mentioned low-lying tracts, the ground is without cockles, but on descending to these depressions the deposit of shells is suddenly reached. This is true in the case of the north end of the depression, Jaksi Klich, which, though 15 miles from the Aral Sea, was formerly joined with it by a channel, and equally true of the steepest parts of the bank, as, for example, where the southern slopes of Togusken rise almost vertically from the water's edge. I have also every reason to believe that those parts of the Ḳara Ḳum which I did not visit are also without Aral shells. I made particular and independent inquiry from many of the Kirghiz who live in various parts of the

Ḳara Ḳum, showing them cockle shells (*Aigulaḳ*), and asking if they knew any localities where they were found. They all said that they had seen them at Jaksi Klich, Jaman Klich, and Shumish Kul, which are in the depressed regions, but they had never seen them in any other locality. I made special inquiry with regard to Aris Kul, which is marked on the maps as a considerable depression lying to the east of Ḳara Ḳum, and I was told by several persons, independently, that no such shells were found there. For these reasons, it seems that, though the Aral Sea has retired within recent times from such an area as would be covered by it if its level were about 15 feet higher than it now is, yet it cannot be shown that it has continuously receded from an area much larger than this. If it ever extended over the Ḳara Ḳum northwards to Tschalkar, this must have been in the remote past, and its disappearance from the definite shell-covered area must have been a comparatively recent event, not continuous with its disappearance from the larger and vaguely defined region which it is supposed to have covered in later Tertiary times.

Special Account of the Basins Jaksi Klich, Jaman Klich, and Shumish Kul

The region where the greatest exposure has taken place is situated to the north and east of the Sary Cheganaḳ. Here the sandy coast slopes very gradually to the sea, and at the post-station Alta Ḳuduḳ, for example, the shell-covered region is about 3–4 miles wide. But at Aḳ Jalpas there is a dry channel running up from the bay, which divides into two branches, the one running east and north, and the other running south. The latter has a course of about six miles; near Aḳ Jalpas it is about half a mile wide, and is covered with mud, which is impassable after rain. Further south the channel narrows, and in some of the deeper holes in it there is always a little very salt water. This channel runs in a depression between the hills Aḳ Jar and Bultuḳ, and then opens out into a great depression, lying east and west, for a distance of about 8 miles. This place is known to the natives as Shumish Kul. (It is marked on the Russian maps as "Khan Sultan." This name is not known on the spot, though the mountain at the east end of the lake is called Khan Turt.)

The appearance of this lake is very striking. The north and west shores are formed by bare hills, with a few bushes and coarse grass at their base. Thence to the bottom of the lake is a tract of undulating

sand, bearing scanty vegetation. Below the sand a stretch of baked mud is exposed, surrounding the pan of salt which fills the lowest part of the lake. The salt lies in large contorted sheets, overlaying each other like frozen waves of muddy ice. On the eastern and southern

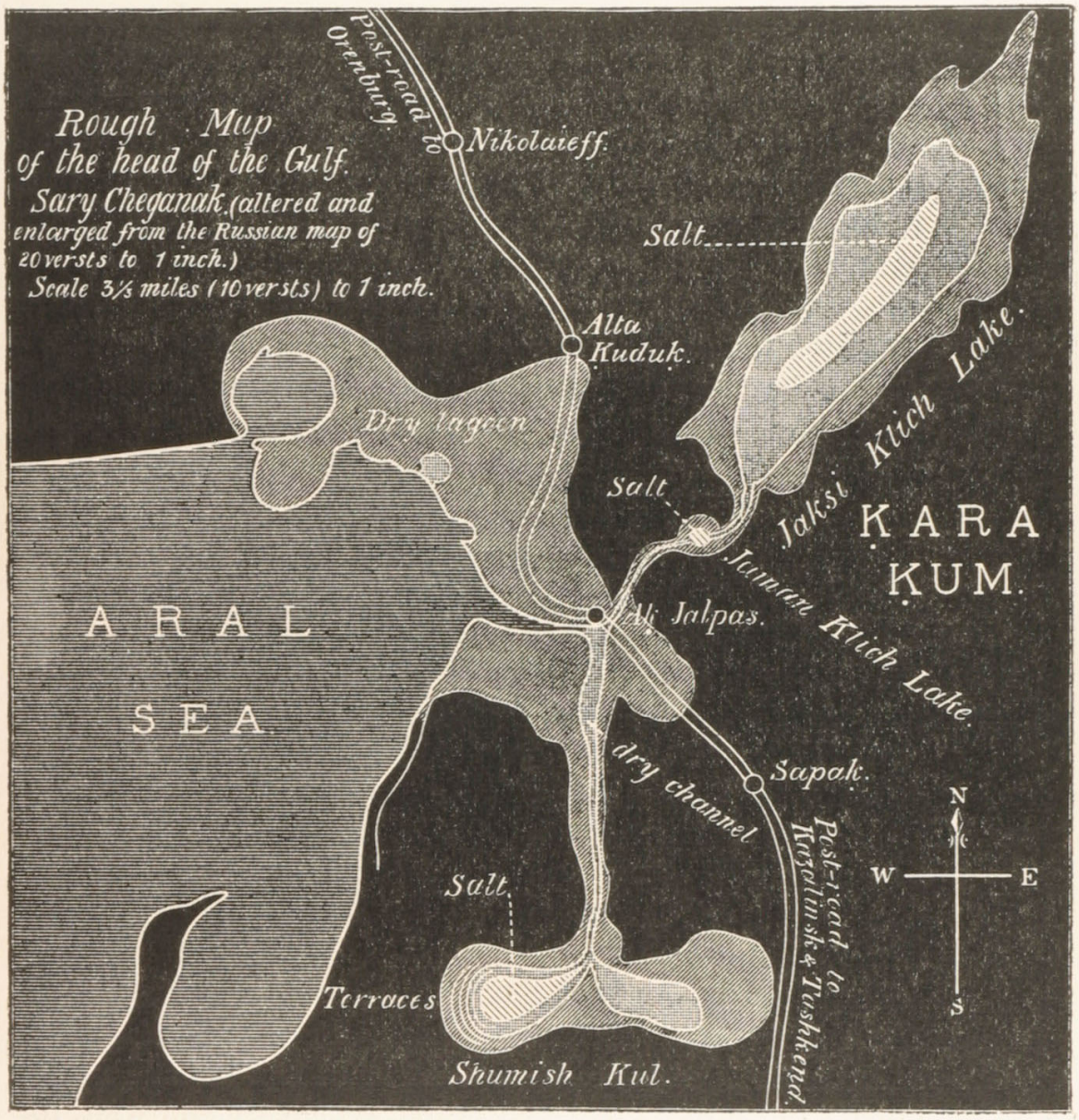


Fig. 1

shores, which shelve away gradually to more distant hills, are great flats of salt mud covered with *Salicornia*, etc.

The biological interest of this place lies in the fact that upon the steep western shore are marked very definite terraces, showing the position of the water at different periods during the progress of the

gradual drying up of the lake. On each of these terraces cockle shells are found in great quantities, having been left there when the water was at the level of the terrace. A series of specimens, therefore, taken from each terrace from above downwards, gives examples of the shells as they were at each stage during the progressive desiccation of the lake. On several of the terraces the shells are paired shells, with the ligaments more or less preserved, placed upon their oral surfaces, just as they were when alive, being kept in position by a crust of sand cemented with oxide of iron. Unfortunately, there is no reliable means of estimating the time which elapsed during the process of drying up. The intervals of time, however, between the formation of the successive terraces were sufficiently long to enable the shells to acquire definite characters, especially of colour and texture, which made it easy to distinguish shells of any one terrace from those of the one above or below it.

The principal terraces are seven in number, but, before describing in detail the condition of the shells on them, it may be well to give a general account of the changes which were produced in correlation to the diminished size of the lake. The principal changes are as follows:

(1) *Diminution in the Thickness of the Shells*, which is first apparent in the shells of the third terrace. It proceeds to such an extent that the shells of the lowest terrace are almost horny and semi-transparent.

(2) *The Size of the Beak is Greatly Reduced.* In the shells of the upper terraces the beak encloses, so to speak, a separate chamber, while in those of the lower terraces it hardly forms a projection on the outside of the shell.

(3) *The Shells become Highly Coloured.* This change and (1) occur almost uniformly. The shells of each terrace are very nearly alike in texture, thickness, and degree of coloration.

(4) *The Grooves between the Ribs appear on the Inside of the Shell as Ridges with Rectangular Faces.* This change first affects only the ribs behind the 8th or 10th, but on the lowest terraces all the ribs are so affected.

(5) On the lowest terrace *the shells diminish greatly in absolute size.*

(6) *The Length of the Shells in proportion to their Breadth Increases.* I use the term "length" to mean the greatest antero-posterior dimension, and the term "breadth" to mean the dorso-ventral measurement at right angles to the length, passing in right valves across the

point of the posterior tooth, and in left valves across the depression into which the posterior tooth of the right valve fits.

It must be remembered that, though the tooth is a fixed point in the morphology of the shell, there is no defined point on the ventral margin which can be determined in each shell for comparison with other shells. Hence, I am aware that the points selected for these measurements are arbitrary, and that they are not taken in absolutely homologous places in every shell. Nevertheless, they are very nearly so, and on the whole they are more satisfactory than any others. The object of these measurements is to obtain an arithmetical conception of the difference in the proportion of length to breadth which is apparent to the eye. This difference in appearance is almost

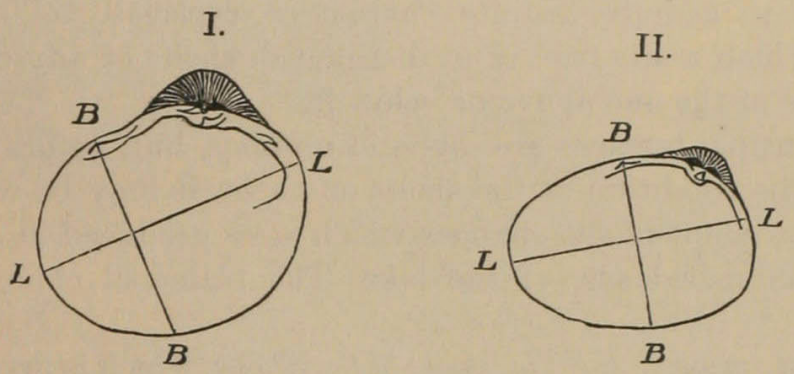


Fig. 2

Diagrams showing the directions in which the length and breadth of the shells are measured:

I. A shell from the shore of the Aral Sea.

II. A shell from Jaksi Klich (inner deposit). *L*, *L*, length; *B*, *B*, breadth.

all due to a change in the proportion which the greatest length bears to the greatest breadth at right angles to it. The measurements, owing to the irregularities of the shell, were made accurate to half a millimetre, and I believe that any difference due to variation in the selection of the exactly comparable morphological point on the ventral edge of the shell would be found to be within this limit of error. I am also aware that conchologists use the term length for the shorter of these two measurements; but, as this appears confusing to the general reader, it seems better in a paper of more general biological interest to use the terms in their ordinary sense. In comparing these shells of the upper terraces with those of the lower, it will be found that the greatest length is greater in proportion to the greatest width than it is in those shells which have been exposed to salter water.

I have made tables which are intended to show this change in the proportions of the shells in a tabular form. The tables bring out three points:

(*a*) That the change in proportions does not occur in all the shells, nor to an equal degree in those in which it is found. Thereby it differs from the changes which occur in the texture and colouring. A few shells may be found in any terrace at Shumish Kul which do not differ materially in shape from normal shells. In the case of Jaksi Klich, however, almost all the shells are affected.

(*b*) The second point noticeable in the occurrence of this variation is that it is far more marked in shells of greater absolute size (that is, presumably, of greater age) than in smaller and younger ones. This fact is brought out in the second column of the tables.

(*c*) The third fact which appears on comparing the averages is that the lengthening of the shells occurred slightly in the shells of the second terrace; increasingly in those of the third and fourth; reaching a point in the fifth terrace which is practically not afterwards exceeded in shells found as much as 30 feet lower, though the changes in texture, etc., had greatly progressed in these latter. Evidence will be given, moreover, which tends to show that this lengthening of the shells is more probably due to some other consequence of the diminished size of the lake than to the increase in saltness; for example, to its increasing shallowness and consequent high average temperature in summer. Examples will be given of cockles from lagoons both of the Aral Sea and in Egypt, which, while differing entirely from those of these salt lakes in general appearance, are yet like them in the proportion of length to breadth. The whole question will be fully considered after the specimens have been described. The shells on the several terraces may now be described in detail.

First Terrace. The shells on the first terrace were, no doubt, living at the time when the Aral Sea was connected with this series of lakes and, perhaps, also for a short period after its separation from them. They lie at the foot of the hills coming down to the lake, and, though mostly covered with earth, it was possible to get plenty of them, especially among the *débris* thrown out by burrowing animals. They are, for the most part, smallish shells, being chiefly 19 mm. to 24 mm. in length. They are thick shells, pale in colour, having from 18 to 22 ribs, the region behind the 11th to 14th ribs being purplish in colour.

No paired shells were found at this level. In 30 shells, all between

21 mm. and 16 mm. in length, the average ratio of length to breadth is 1 : 0·799; that is to say, that the average breadth of a shell 20 mm. long would be 15·98 mm.

The Second Terrace. This is a flat about 50 paces across. Upon it are two well-marked ridges of shells, the lowest of which is about 10 feet below the level of the first terrace. These ridges were obviously formed by the casting-up of shells on the beach during gales, as may be seen on the shore of the Aral Sea in many places (Meregen Sai, etc.). They contain no paired shells with ligaments, such as are found lower down in places where the bottom of the lake has been exposed and not afterwards disturbed.

Shells on this terrace were found of the maximum length of 26 mm. They have from 18 to 21 ribs, the region behind the 11th to 16th being purplish in colour. In 20 shells taken from the lower of the two ridges of shells on this terrace the average ratio of length to breadth is 1 : 0·770 in shells between 26 mm. and 20 mm. in length, and 1 : 0·782 in shells between 21 mm. and 16 mm. in length; that is to say, that among shells similar in size to those of the first terrace the average breadth of a shell 20 mm. long would be 15·64 mm. The shells do not differ materially in consistency from those of the first terrace (*vide* Table of Comparative Weights); they are, however, slightly more highly coloured.

The Third Terrace consists of a strip of small sand-hills about 180 yards wide. The division between it and the region which I have called the fourth terrace is not sharply defined, but is indicated by a ring of old tamarisks. Such rings of tamarisks occur round many of the salt lakes of this steppe, and always show that the water stood at a definite level below them for a sufficiently long period to influence the vegetation. Some of the lakes in the Turgai district were surrounded by several concentric rings of tamarisks, showing several distinct periods in the progressive drying up of the water. This ring of tamarisks stands at a level about 20 feet below that of the ridge of shells which marked the lower limit of the second terrace. Amongst the bases of these sand-hills are many cockles *in situ*, with their ligaments preserved, indicating that this part of the shore remains as it was when it formed part of the bottom of the lake. The shells on this terrace differ from those of the second terrace, being thinner, and showing that appearance of grooving on the inside of the shell which was referred to above (4). In shells of this terrace the grooving is not much marked in the case of ribs anterior to about the 11th.

The number of ribs and distribution of colour are as they were in the last terrace.

In 30 shells between 22 mm. and 18 mm. long the average ratio of length to breadth was 1 : 0·751; that is to say, that the average breadth of a shell 20 mm. long would be 15·02 mm.

The Fourth Terrace is like the last, in that it is a stretch of shelving sand about 100 yards across, falling about 10 feet in level. On it also are many paired shells *in situ*. These shells differ considerably from those of the third terrace, being much thinner and more highly coloured (*vide* Table of Weights). The grooving on the inside of the shells is generally well marked in all behind the 7th rib.

There are generally only about 17 to 19 well-marked ribs, the remainder being slightly indicated on the purple posterior surface of the shell. Most of the shell is purple behind about the 11th rib, and the whole shell is suffused with pinkish purple (see Pl. I, fig. 4).

In 30 shells whose lengths vary between 26 mm. and 18 mm., the average ratio of length to breadth is 1 : 0·730, and, taking 30 shells from 16 mm. to 21 mm. long, this average ratio is 1 : 0·735; that is to say, that the average breadth of a shell 20 mm. long would be 14·7 mm. The beaks are reduced in size.

The Fifth Terrace is a similar stretch of sand; it is 200 yards wide, falling nearly 20 feet, and upon it are very many paired shells placed on their oral faces, like the others. These shells are much thinner than those of the fourth terrace. They have 15 to 17 well-marked ribs, and almost the whole shell is purple in colour in some specimens, but in others the first 3 ribs remain yellowish. The ribbing on the inside of the shell is generally apparent behind the 4th or 5th rib. The beaks are still further reduced in size.

In 30 shells between 27·5 mm. and 21 mm. in length the average ratio of length to breadth is 1 : 0·731; and in 30 shells between 21 mm. and 16 mm. long this average ratio is 1 : 0·743; that is to say, that the average breadth of a shell 20 mm. long is 14·8 mm., not materially differing from those of the last terrace. This terrace ends with the shelving sand. Below it are mud flats, the upper part of which is covered with heaps of muddy sand, cemented together with salt, forming the *Sixth Terrace*. The shells upon it, however, do not differ materially from those of the last, except, perhaps, in being rather thinner.

Below it is the lowest level at which shells are found (*Seventh Terrace*). This level is 8 to 10 feet below that of the fifth terrace, and

distant from it about 200 yards. Upon this lowest level are several (five) concentric ridges, composed of shells washed up and partially cemented together with oxide of iron. The shells of which these ridges are made are like those of the fifth and sixth terraces. On the flat mud between these ridges, especially between the fourth and fifth, are great numbers of small paired shells placed on their oral faces. These shells are those of the last cockles which lived in the lake before it was dried up. At this time the water must have been very salt indeed, as the salt bed itself is about 5 to 6 feet lower and 300 yards distant.

The shells are very small. The largest paired shell found in this place was 21 mm. long. They have 14 to 15 distinct ribs, are very thin, and of an almost uniform purple colour. The grooves between the ribs are all marked on the inside of the shell as ridges with flat sides. The beaks project very little from the general curve of the shell.

The average ratio of length to breadth in 30 shells the lengths of which were between 16 and 21 mm. is 1 : 0·725; that is to say, the average breadth of a shell 20 mm. long is 14·50 mm., as compared with 15·98 mm. in the case of the shells of the highest level.

Dreissena polymorpha. At one side of the lake on the level of the third terrace were found many shells of this form, which did not differ from those of the Aral Sea. The same is true of *Hydrobia ulvæ*, which was found in fair quantities on most of the terraces.

Jaksi Klich

This is the largest, superficially, of the three dry lakes containing cockles. Its length is about 10 miles, and its breadth 3 miles. It differs from Shumish Kul in being comparatively shallow. While the former must have been nearly 60 feet deep at the time of the separation from the Aral Sea, the basin of Jaksi Klich cannot have been more than 15 to 20 feet deep. There is not in it a distinct series of terraces, as at Shumish Kul, but the shells occur in two chief deposits, the one marking the original high level of the water, and the other forming a band round the salt which now fills the bottom of the lake. Moreover, owing to the fact that the shells of the outermost deposit are almost all single valves, and not paired shells *in situ*, as at Shumish Kul, a good deal of mixing has become possible amongst them, which was, no doubt, facilitated by the shallowness of the lake; as the banks are so flat that at the time when the lake was low it may

have happened that under a strong wind the water was driven upon the shore even as high as its original level. Hence it results that the upper deposit of shells at Jaksi Klich is more mixed in character than the deposits hitherto described. I will first describe the condition of the shells found at the bottom of the lake. They occur there in enormous numbers, being for the most part washed up into banks. A certain number of paired shells occurs between the ridges. Their texture is uniformly thin and papery, and they are very highly coloured, thus resembling the shells of the lower terraces of Shumish Kul, especially those of the sixth terrace. Their length is very great, and this feature is found in almost every individual shell. While they thus resemble in many respects the shells from the salter levels of Shumish Kul, they yet have several features peculiar to themselves, especially the enormously greater degree to which they are elongated; also, though their colour resembles the Shumish Kul shells in being much brighter than that of ordinary Aral Sea cockles, it has a character of its own, which would make it impossible to mistake a shell from either locality.

As will be seen in the tables, the average ratio of length to breadth in 30 shells varying in length between 30 mm. and 25·5 mm. is 1 : 0·660; and in 30 shells varying in length from 25·5 mm. to 19 mm. is 1 : 0·682. It will be seen, therefore, that the increased proportional length is greater in these shells than in any others that were obtained.

The size of the beaks is reduced, just as in the case of the Shumish Kul shells. The shells of the outermost deposit at Jaksi Klich are, as stated above, rather mixed in character. I found, however, one locality towards the southern end of the lake where the bank was comparatively steep, and from this place I obtained a fairly uniform sample. These shells are thin as compared with cockles of the Aral Sea, but thicker than those of the lower deposit of Jaksi Klich. From the latter they differ also in not being highly coloured and in having the beaks fairly developed, though diminished relatively to those of normal Aral shells. As will be shown hereafter, they very closely resemble those shells which were found on the shore of the lagoon Abu Kir, in Egypt; the length of these shells is as great in proportion to their breadth as it is in those of the fourth or fifth terrace at Shumish Kul. The average ratio of length to breadth in 30 shells varying in length between 22 mm. and 17 mm. is 1 : 0·740; that is to say, that the average breadth of a shell 20 mm. long is 14·8 mm.

Many examples of *Hydrobia ulvæ* were found amongst these modified shells, but they do not differ from those of the Aral Sea.

In attempting to realise the conditions under which the cockles lived in Jaksi Klich before the separation of this series of lakes from the Aral Sea, the fact of its situation must be borne in mind. It was a large lagoon, ten miles long and three miles broad, very shallow, and connected with the main body of the Aral Sea only by a narrow and shallow channel at Aḳ Jalpas. Hence the conditions of life in it, in a climate which undergoes the greatest extremes of heat and cold, must have been always very different from those prevailing in Shumish Kul, which had a considerable depth, and so must have maintained a much more constant temperature.

Before, therefore, the communication between the lakes and the Aral Sea was interrupted it is clear that the water of Jaksi Klich must have been sometimes very hot, and, from the consequent evaporation, it was probably in summer much salter than the nearest parts of the Aral Sea. In view then of the obvious correlation between the effects of the diminution in size of Shumish Kul and the increase in the proportional length and thickness, etc., of the shells found there, it appears reasonable to ascribe these appearances in the shells of the outer deposit at Jaksi Klich to similar causes, and these must of necessity have existed, consequent upon the peculiar situation and shallowness of the basin.

All these appearances, as has been shown, became greatly intensified in those shells which lived in it during the period after the separation from the Aral Sea.

Besides the shells in these two deposits, there were found at Jaksi Klich a few shells of an entirely different character. These were very large and very thick shells, generally occurring in pairs, more or less buried in the sand, though without ligaments. The length of these shells was about 30 to 35 mm.; they almost all show the feature of great proportional length and large beaks, and were always found in groups of ten or twelve, lying between the outer and inner deposits. These shells are all much worn. I shall allude to these shells as "great shells." Similar shells will be shown to have occurred at Jaman Klich, on the sand flats between Jaman Klich and Shumish Kul, in a small dry lagoon lately separated from the Aral Sea, and in the old deposits at Abu Kir (Mandara, Pl. I, fig. 12). Taken in connection with these cases of the occurrence of such shells, I think that there can be little doubt that shells of this type are connected with life in

shallow lagoons opening out from a sea. All the five localities in which they were found were of this kind, and none were ever found by me anywhere else. On the shores of the Aral Sea and at Shumish Kul none occurred.

Jaman Klich

This is the smallest of the three dry lakes. It was little more than a large pool formed by a widening and deepening of the channel which connected Jaksi Klich with the Aral Sea. At the time when it was full of water its diameter was about half a mile, and its depth 15 to 20 feet. The bottom of the lake is covered by a sheet of salt about 300 yards across. The shells upon the upper part of its shore do not differ materially from those of the Aral Sea, being thick shells with large beaks and little colour. Their proportional length is rather greater than that of the Aral Sea shells. There is little or no ribbing on their inner surfaces.

The shells at the bottom of Jaman Klich are thin, highly-coloured shells, with much ribbing on the inside and beaks greatly reduced in size. They are greatly elongated, though less so than the shells of Jaksi Klich. The average ratio of length to breadth in 30 shells varying in length between 24 mm. and 16 mm. is 1 : 0·726, being practically the same average ratio as that in the shells at the bottom of Shumish Kul.

Amongst these shells were great quantities of *Dreissena polymorpha*, which, though, as always, very variable in shape, did not differ in any uniform manner from those of the Aral Sea.

At the bottom of Jaman Klich is a considerable number of "great shells." They are like those of Jaksi Klich and are much worn.

On the flat between these two lakes and Shumish Kul are many shells strewn. They are, in all respects, like those of the upper deposits at Jaman Klich, and in no way remarkable. There are amongst them a few "great shells," but no thin or highly coloured ones, which occur only in the three lake beds.

Cockles of the Aral Sea

In the Aral Sea itself, the cockles are of very uniform character. They are fairly thick shells (see Table of Weights). The anterior 10 to 11 ribs are generally white, and the remaining 6 or 8 bluish or brown.

There are no "great shells" among them, nor any thin and highly coloured ones.

The average ratio of length to breadth in 30 shells of the Aral Sea varying in length between 22 and 18·5 mm. is 1 : 0·761.

The beaks in every case are large and well developed.

On the west shore of the Sary Cheganaḳ, near Alta Ḳuduḳ, is a small dry lagoon, which had once communicated with the Aral Sea. It was about half a mile wide and had been about 2 to 3 feet deep. In it were many cockle shells; nearly all of these were "great shells," the remainder being shells of the ordinary Aral type.

This completes the description of the cockles of the district of the Aral Sea. It has been shown that in each locality a particular type prevails, which varies hardly at all as regards texture and colour, and that, though the individuals of each type vary considerably in shape, yet there is a distinct preponderance of long shells among those which have been exposed to the conditions incidental to the drying up of the lakes in which they were living; and that, in the case of each of three lakes, the changes undergone by the shells have been similar, though different in degree.

I will now describe the shells found in the lagoons near Alexandria, and then compare them with those of the Aral Sea district.

The Cockles of Lake Mareotis and Lake Abu Kir

At the present time (1888)[1] Lake Abu Kir is a shallow salt lake, having an area of about 20 square miles and a depth of about 1 to 2 feet at most. In April, 1888, its specific gravity was 1·05. No living shells were found in it but its shores were covered with great quantities of uniformly small, thin, highly coloured shells (see Pl. I, fig.10). These shells are elongated in the same way as those of Jaman Klich, which they closely resemble.

The average ratio of length to breadth in 30 of these shells varying in length from 24 mm. to 19·5 mm. is 1 : 0·738. (For average weight see Table of Weights.)

These shells are plainly those of the cockles which last lived in the lagoon of Abu Kir, and it may be supposed that they lived in it under conditions not very different from those now prevailing. It is difficult to assign with certainty any cause for their extinction, but this may perhaps have been due to an unusually dry season following on a low Nile.

[1] Abu Kir was pumped out in May, 1888.

The lagoons of Abu Kir and of Mareotis are separated from the sea by a narrow bank, partly of limestone and partly of sand; and from the presence of marine shells in the lagoons it is clear that they formerly communicated with the sea. The cockles, therefore, of these lagoons are the descendants of those of the Mediterranean.

There is some reason for supposing that they passed through another condition between that of the Mediterranean type and that found on the shores at Abu Kir; for at Mandara and at other points on the shore of the Lake Abu Kir, where cuttings have been made, deposits of great quantities of shells almost invariably occur at a varying depth below the surface.

These shells are nearly all of the very large and thick type spoken of above (*vide* p. 48) as "great shells." From the great abundance of shells of this type in the deposits below the present bed of Abu Kir, it seems clear that they were numerous in the locality for a long period. As they are entirely absent among the shells now lying on the shores of the lake (namely, those which were the last inhabitants), I would suggest that these "great shells" perhaps lived there in the period when the sea communicated with the lake. This becomes still more probable in connection with the fact of the occurrence of similar shells at Jaksi Klich, Jaman Klich, and on the flats between them and Shumish Kul, for at the time when these localities were under water and connected with the Aral Sea the conditions in them could not have been very different from those prevailing in the lagoon of Abu Kir when it was open to the Mediterranean. The shells, then, of Abu Kir are of two kinds:

(1) Shells of animals lately extinct, which lived in a lagoon of water having a specific gravity of about 1·05; these shells show the same variations from the "normal" type as those of the Aral district living under similar circumstances.

(2) "Great shells" occurring in a more or less definite bed below the level of the present lagoon, the origin of which is uncertain, but which were probably living when the lagoon was open to the sea.

Mareotis and the Fresh-water Lakes at Ramleh

The Lake Mareotis is now divided by an embankment into an eastern and western part, which differ from each other entirely.

The western lake is full of red brine-water, and beneath the water is a permanent crust of salt.

I did not succeed in finding any shells on the shore of this portion,

though, no doubt, cockles lived in it before the changes were made which have led to its present condition.

The eastern lake contained about 1 to 3 feet of water in most places in April, 1888. A very small stream of sea-water runs into it near Meks. At the time of my visit its density was about that of the Mediterranean, but it, no doubt, varies greatly with the time of year

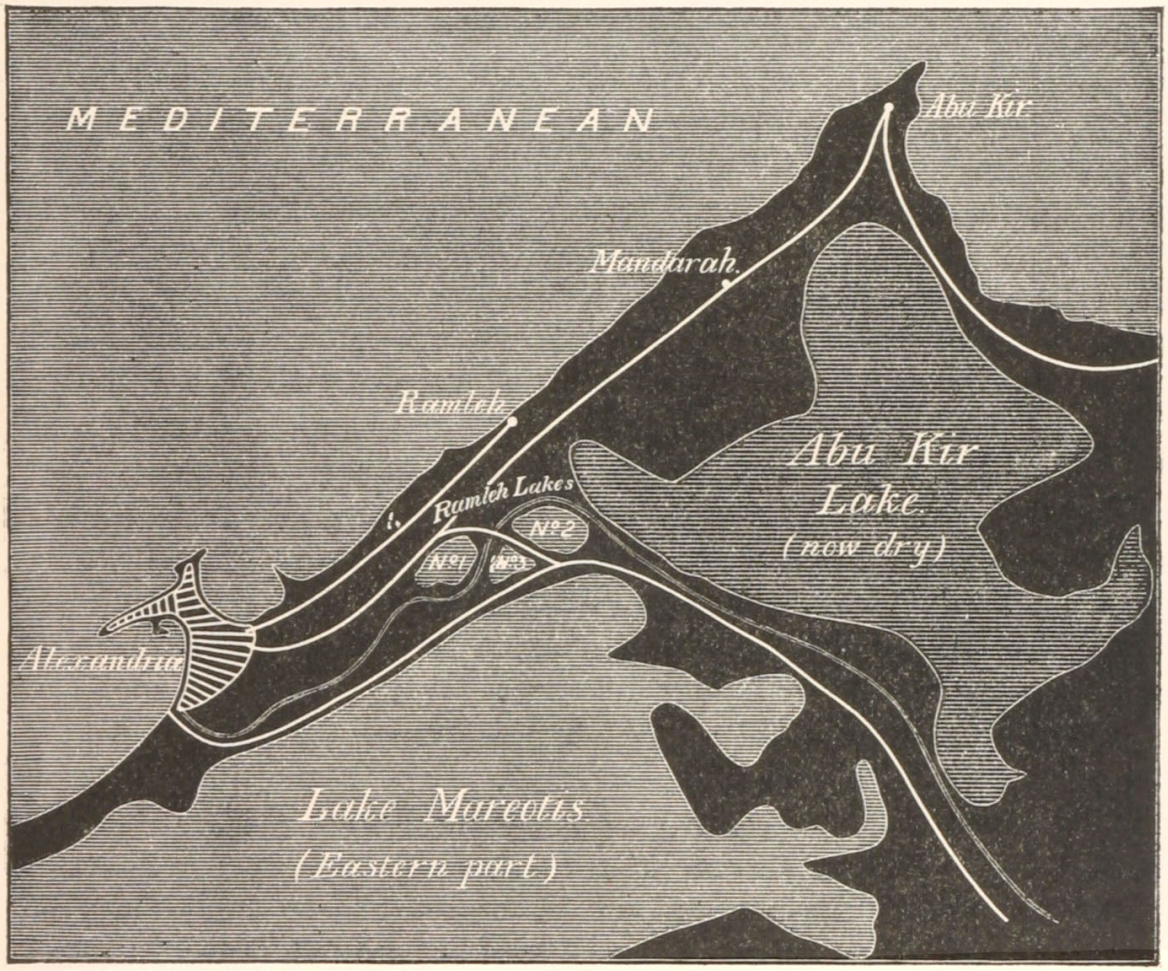


Fig. 3. Rough map of Lake Mareotis, together with Abu Kir and the three Ramleh lakes.

and the state of the Nile. The lake, which lies 8 feet below the surface of the Mediterranean, is stated to have been nearly dry at the end of the last century, but in the course of military operations in 1801 it was again opened to the sea by the English. Possibly, then, the shells now found on its shore are the descendants of those then admitted from the Mediterranean. Another opening was lately made from the sea, but has been nearly closed, the small stream of water from the sea mentioned above being due to this opening.

At high Nile the level of the lake rises, owing to the infiltration of fresh water, and probably it is brackish at this season. From these considerations and from the many vicissitudes that the lake has undergone, it is clear that nothing can be stated with certainty as to the conditions which have prevailed in it for any length of time, beyond the fact that it has always been a large shallow lagoon, and that a large quantity of fresh water from the Nile has been poured into it every year.

I did not find any live cockles in it, and am disposed to believe that they are extinct in it, having probably died in consequence of some of the sudden changes which have befallen the lake.

The shells found on the banks of Mareotis are, like those of Abu Kir, of two kinds:

(1) Old shells, for the most part very large and not greatly differing from the "great shells" of Abu Kir. These occur especially on the cliffs near the road running beside the lake on its south-west shore. The shells here occur at a level several feet above that of the lake. These shells are much worn, and may be regarded as being in a semi-fossil state. They are possibly shells which lived in the lagoon when it was open to the sea.

(2) Shells found in great numbers on the shores of the lagoon. These are nearly all paired valves with their ligaments. They are all of a most definite type (*vide* Pl. I, fig. 11), being moderately thin shells, having generally the anterior 6 to 10 ribs yellowish-white in colour, and the posterior 7 to 12 bluish or chocolate coloured; the inside of the shells is much ribbed; the posterior part is generally chocolate colour, and sometimes the whole interior of the shell is so coloured. Many of the shells have bands of dark colour running transversely to the ribs. The shells are nearly all elongated. The average ratio of length to breadth in 30 shells varying in length between 27 mm. and 20 mm. is 1 : 0·680; as in other samples, the elongation is more marked in large shells than in small ones.

The beaks are rather variable, but in most shells they are low.

The peculiarities in colour of these shells are so definite that they could not possibly be mistaken for the shells of cockles from any other locality.

Amongst these modern shells are a few of the old semi-fossil shells mentioned above, which, however, are so different from them, being bleached and worn, that they may be at once distinguished.

Ramleh Lake No. 1

By the formation of the Mahmudiyeh Canal, which was begun in 1819, a small piece of water was separated from the great Lake Mareotis, in the neighbourhood of Sidi Gaber station.

This lake is about a mile in greatest diameter, and its water is at the present time fresh, receiving much waste water from the irrigations, and is perhaps 10 to 12 feet deep in the middle, though shallow at the sides. The bottom at the sides is sand, and in the middle is mud. Great quantities of cockle shells lie on the bottom of the lake, but I found no live animals, and believe that they are extinct. These shells have a definite character, being thick and coarse in texture, with 14 to 16 anterior ribs, white, and from 3 to 5 posterior ribs, chocolate colour. The region of the anterior ribs (6 to 10) is generally not ribbed on the inside of the shell. The insides of the shells have a peculiar white colour. The shells are very long in proportion to their breadth, and most of them have one or more deeply marked lines of growth. The beaks are high and large. Amongst the smaller shells found here are some few which are extraordinarily thick.

Ramleh Lakes Nos. 2 *and* 3

By the construction of the railway from Alexandria to Cairo, 1855, a second part of Mareotis has been cut off by an embankment, and the lake thus formed was again divided into two by the embankment recently made to connect the Cairo railway with the Ramleh line. In this way two lakes have been formed, an eastern (No. 2) and a western (No. 3). Both of these are fresh, receiving the water from irrigations. In the western lake I found no cockles at all, either dead or living, though the water is crowded with Prawns (*Palæmon*, sp. ?).

In the eastern lake (No. 2) were great numbers of living cockles. In texture these shells resemble those of Ramleh Lake No. 1, though the tendency to ribbing on the inside was not so much marked, being generally slightly present behind the 10th to 12th rib. The colour of the outside of the shells is yellowish-white almost all over, but on the inside the region of the posterior 3 to 6 ribs is chocolate colour, but the rest of the inside of the shells has the same bright white colour as in Ramleh Lake No. 1. The proportion of length to breadth is very great in these shells. In 30 shells varying in length between 29 mm. and 16·5 mm. the average ratio of length to breadth is 1 : 0·657, and in 30 shells varying in length between 21 mm. and 17 mm. this average ratio is 1 : 0·665. It is a remarkable fact that in the case of

these shells the increased proportional length is almost as much marked among the small shells as it is amongst the large ones, and, as may be seen in Table VI (*a*), this feature is present fairly uniformly in nearly all the individuals.

Another character of these fresh-water shells is the frequent occurrence of specimens with the free ventral margins of the shell bent inwards, as shown in Pl. I, fig. 13.

Recapitulation (*Mareotis and Ramleh Lakes*)

The shells found in the Mareotis and Ramleh district were of four kinds: (1) ancient shells, like the ancient shells of Abu Kir; (2) shells lately extinct (?) in Mareotis itself. Though the conditions under which these animals lived cannot be positively stated, it is nevertheless clear that they lived in shallow water, and that this water received in winter a great volume of fresh water from the Nile, being then probably brackish, while it is likely that in summer it was rather salter than the sea.

The shells having lived under these conjectural conditions have definite characters, being long, thin, highly coloured shells.

From them are descended independently (3) the cockles of Ramleh Lake No. 1, and also (4) the cockles of Ramleh Lake No. 2. Both (3) and (4) have been living in more or less completely fresh water for some time, and, on comparing them with (2), they will be found to differ from them similarly, and to resemble each other in most respects. They are both fairly thick and coarse, and the high colour of the Mareotis shells is much reduced in (3), and still more so in (4).

The feature of great proportional length remains in both.

As was found in the case of the various samples of Aral shells, the samples of each locality are distinct and easily recognisable, but, excepting a slight difference in colour, (3) and (4) are very nearly alike. A few specimens among (2) resemble in colour those of (3), but they are quite different in texture.

Conclusion

The importance of these observations lies in the fact that, by examining and comparing the shells, an opportunity is given of observing the origin of a set of structural variations in correlation to, and perhaps in consequence of, environmental changes which are to some extent ascertained. The first point which is to be noticed is that the shells of each sample, whether it be from a separate lake or only from a particular terrace, are more like to each other than to the

shells of one of the other lakes, or to those of another terrace in the same lake as at Shumish Kul, where the shells of each terrace have a distinct appearance and character of their own, and may easily be known from the shells of higher or lower terraces.

The next feature of importance is the fact that, in the four independent cases—Shumish Kul, Jaksi Klich, Jaman Klich, and the Egyptian lagoon Abu Kir[1]—the shells which have lived under similar conditions, *i.e.*, in very salt water, have become like each other, having the characters of thinness, high colour, small beaks, ribbing on the inside, and great relative length. In view of these four instances of similar variations occurring under similar conditions, it seems almost certain that these conditions are in some way the cause of the variations. Similarly, in the case of the two groups of cockles from Mareotis which have been isolated and exposed to fresh water in separate lakes, the result has been to produce a form of shell in both cases which is practically the same. Cases of this kind, in which it is possible to observe the appearance and progress of a variation through successive generations in the same place, are so rare that it has seemed worth while to describe these shells in detail. The mode of occurrence of the shells in terraces at Shumish Kul provides an almost unique opportunity for beholding the gradual succession of these changes. If, then, it is admitted that the structural changes in the shells are to be regarded as the consequence of the environmental changes in the water of the lake, the question arises to what extent these structural changes follow directly on the changed circumstances, and how far they may not be due to the natural selection of a different type as the fittest to live in the altered state.

Now, while the cases given above do not give a definite answer to this question, they nevertheless contribute something towards it. The chief qualities which appear in the shells which have been exposed to the increased saltness are comparative thinness, high colour, and increased length, together with diminished beaks. If, then, it is supposed that shells having these qualities were being gradually chosen by natural selection as the fittest for the new conditions, it would be expected that in each terrace these several attributes would be found in varying degree among the individual

[1] Amongst the shells in the Cambridge University Museum collected by Mac Andrew are a few cockles from a lagoon at Tunis, which show the same features. Though, in the absence of further information as to the locality from which they were brought, nothing can be positively stated, yet it is likely that they afford another instance of a similar variation under similar conditions.

shells—that some would be thick and some thin, some long and some short, etc.; on the other hand, if the new qualities were the result of the new conditions, then it would be anticipated that the shells of each terrace would be all nearly similar in texture and shape. The more uniformly any of the new variations are found among the individuals, the more probable is it that they are due to the direct action of environmental change rather than to natural selection; but a new quality, which is found in the several individuals to a greatly varying degree, cannot be held to be shown to be the direct result of the conditions, even though it be found to be increasingly more marked on the average in successive generations as the conditions to which it is supposed to be due become more intense. Now the variations formed among these shells are of two kinds. The variation in proportional length, though becoming more and more marked in the shells which have been exposed to salter water, is not found in all the individuals (*vide* tables); on the other hand, the variations in the quality, texture, and colour of the shell are found developed to nearly the same degree among all the individuals of successive terraces. Hence it may be fairly supposed, in the case of these latter variations, that they are really due to direct environmental change. The same also is true of the shells from the fresh-water localities, the texture and colour of which are practically uniform, while a good deal of variation is found in the shape, though the general prevalence of the long type is clear. In view of the manifest connection between variation in the texture, etc., of the shells and the conditions in the lake, it would be interesting to know more clearly the mode of action of these conditions in producing those effects, but as to this it is difficult to make a conjecture. No doubt they are the result of changes in the nutrition of the animals, but more than this does not seem clear. It can scarcely be supposed that the thinness of the shells was due to a deficiency of lime in solution in the water, since this would rather increase in relative amount with the evaporation. Moreover, the shells from the two fresh-water lakes at Ramleh are fairly thick. Neither can the deficiency in the amount of the shells be due to general starvation, since there is no diminution in absolute size at Shumish Kul, except in the case of the shells of the lowest level, which do appear generally ill-nourished; while, at Jaksi Klich, those shells which have become thin and papery from the desiccation of the lake are, on the whole, absolutely larger than an average sample of shells from the Aral Sea.

It may here be remarked that the striking similarity between the shells which had been exposed to very salt water at Abu Kir and those of the salt lakes of the Aral region has features of special interest, since not only have the similar conditions prevailed in producing two forms closely resembling each other, but this has been achieved, though the animals subjected to the influence were at first unlike and had had a very different history. For even supposing that the cockles in the Aral Sea were originally derived from those of the Mediterranean, which is uncertain, yet the Aral shells have been living for ages in water containing less than a third of the salt contained in Mediterranean water, and the Aral cockle is quite sufficiently different from that of the Mediterranean to constitute a well-marked variety. So that, while the cockles originally isolated in Abu Kir came directly from the Mediterranean, the ancestors of those which were subjected to increased saltness at Jaksi Klich, etc., had been living in brackish water in the Aral Sea for an indefinite number of generations, *yet the resulting forms in both cases are closely alike.*

It is not well to press conclusions of this kind too far, and it may be that unfavourable conditions of some kind quite other than increased saltness may result in producing similar variations. All that can be stated with certainty is that shells exposed to increasingly salt water do change in a particular way, and that they do so with great regularity and uniformity. In the same way it has been shown that the influence of fresh water does not lead to the production of a peculiar type of shell. In the case of the variation consisting in increased proportion as to length, it is especially probable that the cause lies in the general unfavourableness of the conditions. It was shown to be present both in those shells which had been exposed to salt water and in a still greater degree among those which had been living in fresh water. It is not rare to find occasionally shells of cockles from the English coast of similar shape. Nevertheless, the regularity of the presence of this feature among the shells from these abnormal situations is so great as to make it certain that this phenomenon is in some manner due to the conditions. Instances in which it is possible to actually trace the occurrence of variations are so rare that no apology is required for having given so much attention to details which would be otherwise unimportant. In the cases here given it has not only been possible to observe the variations, but also to obtain the actual ancestors of the varying offspring for comparison,

and in the case of the shells of Shumish Kul an opportunity is given of doing this at several successive stages.

I wish to express my thanks to many persons who have assisted me in the course of my investigations, and especially to Sir Robert Morier, G.C.B., British Ambassador at St Petersburgh, who obtained permission for me to travel in Central Asia; to M. Semenow, Vice-President of the Imperial Geographical Society, and to M. Maximovitch of the Botanic Garden, for much valuable information and advice; also to C. A. Cookson, Esq., C.B., British Consul at Alexandria. Moreover, though this page may never reach them, I cannot let this opportunity pass without expressing my gratitude for the courtesy and hospitality which I everywhere met with at the hands of the Kirghiz people.

Tables Showing Variations in the Average Ratio of Length to Breadth in Shells from Different Localities

Explanation. In the first column of these tables the actual measurements of the lengths and breadths of each shell are given in millimetres. The second column is constructed from the first. It shows the number of shells of each length which compose the sample of 30, and also shows the average breadth of shells having the same length. The third column is constructed from the second by dividing the average breadths in each case by the length. The first average ratio is obtained from the third column by multiplying these quantities by the number of shells from which they were derived, adding together these products and dividing the sum by 30.

[In the column in which the breadths are given the figures in brackets show the number of shells having the same breadth.]

Table I. *The Aral Sea*

Measurements of shells in millimetres		Average breadth of shells having the same length			
Length	Breadth	Length	Average breadth	Number of shells	Ratio of length to breadth
22	17·5, 17(4)	22	17·1	5	1 : 0·77
21·5	16	21·5	16	1	·74
21	16(4)	21	16	4	·75
20·5	16	20·5	16	1	·76
20	16·5, 16(4), 15·5(3), 15(4), 14	20	15·4	13	·77
19·5	15·5, 15, 14	19·5	15	3	·76
18·5	14, 13	19	14·8	2	·76
		18·5	13·5	1	·72

Average ratio of length to breadth in 30 shells varying in length between 22 mm. and 18·5 mm. is 1 : 0·761.

Table II. *Shumish Kul*

The First (Highest) Terrace

Measurements of shells in millimetres		Average breadth of shells having the same length			Ratio of length to breadth
Length	Breadth	Length	Average breadth	Number of shells	
21	17, 16	21	16·5	2	1 : 0·77
20·5	16(2)	20·5	16	2	·78
20	16(5), 15·5, 15(2)	20	15·6	8	·78
19	15·5(2), 15(4)	19	15·1	6	·79
18·5	15·5, 15, 14·5, 14	18·5	14·7	4	·79
18	15(3), 14·5(2), 14(2)	18	14·5	7	·80
17·5	14·5, 14	17·5	14·2	2	·81
17	14(5), 13·5, 13	17	13·7	7	·81
16·5	14	16·5	14	1	·84
16	13	16	13	1	·81

Average ratio of length to breadth in 30 shells varying in length between 21 mm. and 16 mm. is 1 : 0·799.

The Second Terrace

(*a*) Shells. *Varying in length between* 21 *mm. and* 16 *mm.*

Measurements of shells in millimetres		Average breadth of shells having the same length			Ratio of length to breadth
Length	Breadth	Length	Average breadth	Number of shells	
21	17(2), 16(2)	21	16·5	4	1 : 0·78
20·5	16	20·5	16	1	·78
20	16(2), 15·5, 15(3)	20	15·4	6	·77
19·5	16, 15·5, 15	19·5	15·5	3	·79
19	16, 15·5(3), 15, 14	19	15·2	6	·80
18·5	14	18·5	14	1	·76
18	15(2), 14·5, 14(3)	18	14·4	6	·80
17·5	14	17·5	14	1	·80
17	14	17	14	1	·82
		16	13	1	·81

Average ratio of length to breadth in 30 shells varying in length between 21 mm. and 16 mm. is 1 : 0·782.

(*b*) SHELLS. *Varying in length between* 26 *mm. and* 20 *mm.*

Measurements of shells in millimetres		Average breadth of shells having the same length			Ratio of length to breadth
Length	Breadth	Length	Average breadth	Number of shells	
26	20	26	20	1	1 : 0·76
25	19(²), 18·5	25	18·8	3	·75
24·5	19	24·5	19	1	·77
24	19, 18(²)	24	18·3	3	·77
23	17(²)	23	17	2	·73
22	18(⁴), 17·5(²), 17(²)	22	17·5	8	·79
21	17, 16	21	16·5	2	·78
20·5	16	20·5	16	1	·78
20	16, 15·5, 15(²)	20	15·3	4	·76
19·5	15·5, 15	19·5	15·2	2	·75
19	15·5(²), 15	19	15·3	3	·80

Average ratio of length to breadth in 30 shells varying in length between 26 mm. and 20 mm. is 1 : 0·770.

The Third Terrace

Measurements of shells in millimetres		Average breadth of shells having the same length			Ratio of length to breadth
Length	Breadth	Length	Average breadth	Number of shells	
22	17, 16(⁴)	22	16·2	5	1 : 0·73
21·5	16·5, 16(⁴), 15	21·5	15·9	6	·74
21	16·5, 16(³), 15	21	15·9	5	·75
20	16(²), 15(³)	20	15·4	5	·77
19·5	15	19·5	15	1	·76
19	15(²), 14·5, 14(²)	19	14·5	5	·76
18	14·5, 14, 13	18	13·8	3	·76

Average ratio of length to breadth in 30 shells varying in length between 22 mm. and 16 mm. is 1 : 0·751.

The Fourth Terrace

(*a*) Shells. *Varying in length between* 21 *mm. and* 16 *mm.*

Measurements of shells in millimetres		Average breadth of shells having the same length			Ratio of length to breadth
Length	Breadth	Length	Average breadth	Number of shells	
21	16·5, 16, 15·5, 15(²)	21	15·4	5	1 : 0·73
20·5	16·5, 16, 15(²)	20·5	15·6	4	·76
20	16, 15, 14·5, 14(³)	20	14·5	6	·72
19·5	15, 14(²)	19·5	14·3	3	·73
19	14, 13·5, 13	19	13·5	3	·71
18·5	13	18·5	13	1	·70
18	14, 13	18	13·5	2	·74
17·5	14, 13	17·5	13·5	2	·77
17	13	17	13	1	·76
16	12·5, 12, 11·5	16	12	3	·75

Average ratio of length to breadth in 30 shells varying in length between 16 mm. and 21 mm. is 1 : 0·735.

(*b*) Shells. *Varying in length between* 26 *mm. and* 18 *mm.*

Measurements of shells in millimetres		Average breadth of shells having the same length			Ratio of length to breadth
Length	Breadth	Length	Average breadth	Number of shells	
26	19	26	19	1	1 : 0·73
25	18	25	18	1	·71
23	18, 17·5, 16	23	17·1	3	·74
22·5	17	22·5	17	1	·75
21	16·5, 16, 15·5, 15(²)	21	15·4	5	·73
20·5	16·5, 16, 15(²)	20·5	15·6	4	·76
20	16, 15, 14·5, 14(³)	20	14·5	6	·72
19·5	15, 14(²)	19·5	14·3	3	·73
19	14, 13·5, 13	19	13·5	3	·71
18·5	13	18·5	13	1	·70
18	14, 13	18	13·5	2	·74

Average ratio of length to breadth in 30 shells varying in length between 26 mm. and 18 mm. is 1 : 0·730.

The Fifth Terrace

(*a*) SHELLS. *Varying in length between* 21 *mm. and* 16 *mm.*

Measurements of shells in millimetres		Average breadth of shells having the same length			Ratio of length to breadth
Length	Breadth	Length	Average breadth	Number of shells	
21	17, 16·5, 16(²), 15·5	21	16·2	5	1 : 0·77
20·5	15	20·5	15	1	·73
20	15·5, 14	20	14·7	2	·73
19·5	14·5, 14	19·5	14·2	2	·73
19	15, 14(⁴), 13·5, 13	19	13·9	7	·73
18	14(²), 13·5	18	13·8	3	·73
17·5	13·5, 13	17·5	13·2	2	·75
17	13·5, 13(²), 12·5	17	13	4	·76
16	13, 12·5, 12(²)	16	12·3	4	·77

Average ratio of length to breadth in 30 shells varying in length between 21 mm. and 16 mm. is 1 : 0·743.

(*b*) SHELLS. *Varying in length between* 27·5 *mm. and* 21 *mm.*

Measurements of shells in millimetres		Average breadth of shells having the same length			Ratio of length to breadth
Length	Breadth	Length	Average breadth	Number of shells	
27·5	19	27·5	19·5	1	1 : 0·70
26	20, 19, 18	26	19	3	·73
25·5	17	25·5	17	1	·67
25	19·5, 19, 18·5, 18, 17·5	25	18·5	5	·74
24	19(²), 18·5, 18, 17·5	24	18·4	5	·75
23	17, 16·5(²), 16(²)	23	16·4	5	·71
22·5	17(²), 15·5	22·5	16·5	3	·73
22	17·5, 17, 16·5, 15	22	16·5	4	·75
21·5	16	21·5	16	1	·74
21	17, 16	21	16·5	2	·73

Average ratio of length to breadth in 30 shells varying in length between 27·5 mm. and 21 mm. is 1 : 0·731.

The Seventh Terrace

SHELLS. *Varying in length between* 21 *mm. and* 16 *mm.*

Measurements of shells in millimetres		Average breadth of shells having the same length			Ratio of length to breadth
Length	Breadth	Length	Average breadth	Number of shells	
21	15	21	15	1	1 : 0·71
20·5	15	20·5	15	1	·73
20	15(3), 14·5, 14(3)	20	14·5	7	·72
19·5	13·5	19·5	13·5	1	·69
19	14·5, 14(2), 13	19	13·8	4	·72
18·5	13	18·5	13	1	·70
18	14(2), 13·5(2), 12	18	13·4	5	74
17·5	13, 12	17·5	12·5	2	·71
17	13(2), 12(4)	17	12·3	6	·72
16	13, 12	16	12·5	2	·78

Average ratio of length to breadth in 30 shells varying in length between 21 mm. and 16 mm. is 1 : 0·725.

TABLE III. *Jaksi Klich*

Shells of the outer deposits varying in length between 22 *mm. and* 17 *mm.*

Measurements of shells in millimetres		Average breadth of shells having the same length			Ratio of length to breadth
Length	Breadth	Length	Average breadth	Number of shells	
22	16(3)	22	16	3	1 : 0·72
21	16(3), 15·5, 15(3)	21	15·7	7	·74
20	15(7), 14·5, 14	20	14·8	9	·74
19·5	14(2)	19·5	14	2	·71
19	15, 14	19	14·5	2	·76
18·5	14(2)	18·5	14	2	·75
18	14, 13(2)	18	13·3	3	·73
17·5	13·5	17·5	13·5	1	·77
17	14	17	14	1	·82

Average ratio of length to breadth in 30 shells varying in length between 22 mm. and 17 mm. is 1 : 0·740.

Shells of the Inner Deposit

(*a*) SHELLS. *Varying in length between* 25·5 *mm. and* 19 *mm.*

Measurements of shells in millimetres		Average breadth of shells having the same length			Ratio of length to breadth
Length	Breadth	Length	Average breadth	Number of shells	
25·5	17·5, 17	25·5	17·2	2	1 : 0·73
25	17·5, 17, 16·5	25	17	3	·68
24·5	16(2)	24·5	16	2	·65
24	17, 16(2)	24	16·3	3	·67
23·5	16(2)	23·5	16	2	·68
23	15·5(2), 14·5	23	15·1	3	·65
22·5	16, 15·5, 15	22·5	15·5	3	·68
22	16(2), 15(4)	22	15·3	6	·69
21·5	15·5, 15(2)	21·5	15·1	3	·70
21	14·5	21	14·5	1	·69
20	13	20	13	1	·65
19	14	19	14	1	·73

Average ratio of length to breadth in 30 shells varying in length between 25·5 mm. and 19 mm. is 1 : 0·682.

(*b*) SHELLS. *Varying in length between* 30 *mm. and* 25·5 *mm.*

Measurements of shells in millimetres		Average breadth of shells having the same length			Ratio of length to breadth
Length	Breadth	Length	Average breadth	Number of shells	
30	20	30	20	1	1 : 0·66
29	20	29	20	1	·69
28	19, 17·5	28	18·2	2	·65
27·5	19·5, 19, 18	27·5	17·5	3	·63
27	19(3), 18(2), 17·5	27	18·4	6	·68
26·5	18(2), 17·5, 17	26·5	17·6	4	·67
26	18(3), 17·5, 17(3)	26	17·5	7	·67
25·5	18, 17·5(2), 17(3)	25·5	17·3	6	·67

Average ratio of length to breadth in 30 shells varying in length between 30 mm. and 25·5 mm. is 1 : 0·660.

TABLE IV. *Shells from the bottom of Jaman Klich*

Measurements of shells in millimetres		Average breadth of shells having the same length			
Length	Breadth	Length	Average breadth	Number of shells	Ratio of length to breadth
24	17, 16·5	24	16·7	2	1 : 0·69
23	17, 16	23	16·5	2	·71
22	16(3)	22	16	3	·72
21·5	15·5	21·5	15·5	1	·72
21	15(2)	21	15	2	·71
20·5	15	20·5	15	1	·73
20	14(2)	20	14	2	·70
19	14·5, 14(2), 13·5(2)	19	13·9	5	·73
18·5	14(4), 13	18·5	13·8	5	·75
18	13·5, 13	18	13·2	2	·73
17·5	14, 13	17·5	13·5	2	·77
17	13, 12	17	12·5	2	·73
16	11·5	16	11·5	1	·71

Average ratio of length to breadth in 30 shells varying in length between 24 mm. and 16 mm. is 1 : 0·726.

TABLE V. *Shells from the shore of Mareotis*

SHELLS. *Varying in length between* 27 *mm. and* 20 *mm.*

Measurements of shells in millimetres		Average breadth of shells having the same length			
Length	Breadth	Length	Average breadth	Number of shells	Ratio of length to breadth
27	19, 18	27	18·5	2	1 : 0·68
26	18	26	18	1	·69
25	18(2), 17·5, 17, 16(2)	25	17	6	·68
24·5	17	24·5	17	1	·69
24	16·5	24	16·5	1	·68
23	16(2), 15·5(2), 15(2)	23	15·5	6	·67
22·5	16(2), 15·5	22·5	15·8	3	·70
22	15·5, 15	22	15·2	2	·69
21·5	15	21·5	15	1	·67
21	15, 14(4)	21	14·2	5	·70
20	14(2)	20	14	2	

Average ratio of length to breadth in 30 shells varying in length between 27 mm. and 20 mm. is 1 : 0·680.

TABLE VI. *Ramleh Fresh-water Lake No. 2*

(*a*) SHELLS. *Varying in length between* 21 *mm. and* 17 *mm.*

Measurements of shells in millimetres		Average breadth of shells having the same length			
Length	Breadth	Length	Average breadth	Number of shells	Ratio of length to breadth
21	15, 14, 13·5	21	14·1	3	1 : 0·67
20	14, 13(3), 12·5	20	13·1	5	·65
19·5	13(2)	19·5	13	2	·66
19	13·5, 13(4), 12·5(3), 12(2)	19	12·7	10	·66
18	13(3), 12·5, 12, 11·5(2)	18	12·3	7	·68
17·5	12(2)	17·5	12	2	·68
17	11·5	17	11·5	1	·67

Average ratio of length to breadth in 30 shells varying in length between 21 mm. and 17 mm. is 1 : 0·665.

(*b*) SHELLS. *Varying in length between* 29 *mm. and* 16·5 *mm.*

Measurements of shells in millimetres		Average breadth of shells having the same length			
Length	Breadth	Length	Average breadth	Number of shells	Ratio of length to breadth
29	17	29	17	1	1 : 0·58
28	19, 18	28	18·5	2	·66
27·5	18·5, 18(2), 17	27·5	17·7	4	·64
26	19, 18·5, 17, 16·5	26	17·7	4	·68
25	17·5, 16	25	16·7	2	·67
24	17(2), 16·5, 15·5, 15	24	16·2	5	·67
23·5	15·5	23·5	15·5	1	·65
23	15, 14	23	14·5	2	·63
22	15·5	22	15·5	1	·70
21·5	15, 14	21·5	14·5	2	·67
20·5	13	20·5	13	1	·65
20	14, 12	20	13	2	·63
19·5	13	19·5	13	1	·66
19	12	19	12	1	·62
16·5	11·5	16·5	11·5	1	·69

Average ratio of length to breadth in 30 shells varying in length between 29 mm. and 16·5 mm. is 1 : 0·657.

TABLE VII. *Shells from the Shore of Abu Kir*

Measurements of shells in millimetres		Average breadth of shells having the same length			Ratio of length to breadth
Length	Breadth	Length	Average breadth	Number of shells	
24	17·5, 17	24	17·2	2	1 : 0·71
23	17, 16, 15·5	23	16	3	·69
22·5	17·5, 16·5, 15·5	22·5	16·5	3	·73
22	16, 15·5, 15	22	15·3	3	·69
21·5	15(5), 14	21·5	14·8	6	·68
21	16, 15·5, 15(2)	21	15·3	4	·72
20·5	15	20·5	15	1	·74
20	14·5, 14(5)	20	14	6	·70
19·5	14·5, 14	19	14·2	2	·75

Average ratio of length to breadth in 30 shells varying in length between 24 mm. and 19·5 mm. is 1 : 0·738.

TABLE VIII

This Table gives the results of the previous Tables. The extremes of length of the shells measured for these averages are given in millimetres, and the average breadths are given in terms of the length, which is taken as 1.

		Smaller samples		Larger samples	
Locality	Level	Extremes of length	Average breadth	Extremes of length	Average breadth
Shore of Aral Sea		22 –18·5	0·761		
Shumish Kul	First terrace	21 –17	0·799		
,, ,,	Second terrace	21 –17	0·782	26–19	0·770
,, ,,	Third terrace	22 –18	0·751		
,, ,,	Fourth terrace	21 –16	0·735	26–18	0·730
,, ,,	Fifth terrace	21 –16	0·743	27–21	0·731
,, ,,	Seventh terrace	21 –16	0·725		
Jaksi Klich	Upper deposit	22 –17	0·740		
,, ,,	Lower deposit	25·5–19	0·682	30–25·5	0·660
Jaman Klich	Lower deposit	24 –16	0·726		
Shore of Mareotis				27–20	0·680
Ramleh Lake No. 2 (fresh-water)		21 –17	0·665	29–16·5	0·657
Shore of Abu Kir		24 –19·5	0·738		

Table Showing the Comparative Weights of Shells of Similar Size

For the purpose of this Table twenty shells were chosen from each sample to be compared, as nearly alike in length as was possible.

The first column gives the name of the locality, the second the level, the third shows the extremes of length in millimetres of the shells selected, the fourth column gives the sum of the lengths of the twenty shells, and the fifth column gives the total weight.

Locality	Level	Extremes of length in millimetres	Average length of 20 specimens	Total weight in grammes of 20 specimens
Shore of Aral Sea		21–17	19·2	13·3
Shumish Kul	First terrace	21–17	19·1	14·1
„ „	Second terrace	21–17	19·4	14·5
„ „	Fourth terrace	21–17	19·2	6·5
„ „	Fifth terrace	21–17	18·9	6·1
„ „	Seventh terrace	21–17	19·7	4·6
Shore of Abu Kir		21–17	19·0	6·4
Jaksi Klich	Upper deposit	23–19	20·4	7·8
„ „	Lower deposit	23–19	20·4	5·5
Jaman Klich	Lower deposit	21–17	19·2	5·1
Ancient shells exposed at Mandara		26–21	23·4	24·2
Shore of Mareotis		25–22	23·8	12·0
Ramleh Lake No. 1 (fresh-water)		25–20	21·4	18·3
Ramleh Lake No. 2 (fresh-water)		26–23	24·1	23·6

Explanation of Plate I

Figs. 1–7 represent shells of *Cardium edule* from the successive terraces at Shumish Kul.

Fig. 1. Right valve from the first (*i.e.*, the highest) terrace.
Fig. 2. Right valve from the second terrace.
Fig. 3. Left valve from the third terrace.
Fig. 4. Right valve from the fourth terrace.
Fig. 5. Right valve from the fifth terrace.
Fig. 6. Right valve from the sixth terrace.
Fig. 7*a*. Left valve from the seventh terrace, seen from the outside.
Fig. 7*b*. The same shell as fig. 7*a*, seen from the inside, showing the grooves.
Fig. 7*c*. Dorsal view of an individual from the seventh terrace, showing the reduced size of the beaks.
Fig. 8. Right valve from the lower deposit at Jaksi Klich.
Fig. 9. Right valve from the lower deposit at Jaman Klich.

Fig. 10. Left valve from the edge of the great lagoon at Abu Kir.
Fig. 11. Left valve from the western shore of Lake Mareotis.
Fig. 12. Left valve from the deposit of sub-fossil shells at Mandara.
Fig. 13. *Cardium edule* from the fresh-water lake at Ramleh (referred to in the text as Ramleh Lake No. 2), seen from its oral end.

All the figures were drawn by the Cambridge Scientific Instrument Company. They show the natural size of the shells and their colours as they appear when *wet*[1].

[1] [For the Plate, as it appeared in the *Phil. Trans.*, the figures were reproduced by lithography. Fortunately the original drawings had been preserved, and the present plate represents their colours far more accurately than the one issued in 1889.—Ed.]

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7*b*

7*c*

NOTES AND MEMORANDA

[*Journ. Marine Biol. Ass.*, N.S., I, 1890]

Notes on the Senses and Habits of some Crustacea. In the course of investigations as to the perceptions of fishes, some interesting facts in the natural history of Crustacea have come under my notice. All the Crustacea in the tanks, except *Carcinus mœnas* and *Portunus depurator* are more active by night than by day. Prawns, *Pandalus*, *Stenorhynchus* and *Inachus* generally remain stationary during the day, but will leave their places to hunt for food if any be put in; but *Ebalia*, *Portunus pusillus*, *Porcellana longicornis*, *Galathea andrewsii*, *Virbius varians* and shrimps are rarely visible until night falls, and hardly ever come out by day even to feed. *Eurynome aspera*, though not hidden away like these, being naturally almost indistinguishable from the broken shells, etc., amongst which it lives, seems also never to feed by day. Excepting the shrimps, nearly every individual of the above-mentioned forms has its own place to which it retires when morning comes, and in which it remains during the whole day. One prawn has occupied the same hole for some weeks, and another, which had lived a fortnight in one corner, left it when some mussels were put in, and now sits on the mussels during the day. The distinction then between day and night is of importance to these animals. Such an animal as a shrimp is in fact certain to be caught by keen-sighted fishes if it uncovers itself by day. If shrimps are thrown by day among pollock, they are always eaten unless they reach the bottom of the tank, but there they are safe even if unburied, for the pollock seems unable to see them when on the bottom, and at once gives up the chase. This may or may not be due to their protective coloration. Pollock very rarely take anything off the bottom, and worms and even glistening things like pieces of mackerel are generally left by them if they are not eaten whilst sinking[1]. Moreover, the bottom of the pollocks' tank is made of yellow gravel brought from the Chesil Beach, which in no wise resembles a shrimp.

Wrasses, however, which are especially fond of shrimps, can not only catch them as they sink in the water, but pursue them on the

[1] This can only be true of small pollock, for large pollock are frequently taken with ground baits.

bottom. The sight of the wrasse is particularly keen, and I have often seen a large wrasse search the sand for shrimps, turning sideways and looking with either eye independently like a chamæleon. Its vision is so good that it can see a shrimp with certainty when the whole body is buried in grey sand, excepting the antennæ and antenna-plates. It should be borne in mind that if the sand be fine, a shrimp will bury itself absolutely; digging with its swimmerets, kicking the sand forwards with its chelæ, finally raking the sand over its back and gently levelling it with its antennæ, but if the least bit be exposed, the wrasses will find it, in spite of its protective coloration. Shrimps put into the wrasses' tank at night escaped for some days, hence they must retire to the sand before daylight is strong enough for the wrasse to see them. The knowledge of night and day is therefore of paramount importance to a shrimp, as it is not safe for it to hunt until darkness has come. Strangely enough, it seems that this knowledge is not obtained through the eyes, or at all events not entirely through them, for if the eyes be extirpated, the shrimps will bury themselves during the day, getting up in the twilight and careering about at night just like uninjured shrimps. On one occasion (7 p.m., August 4th) I noticed that the blind shrimps in a tub were lifting themselves out of the sand exactly at the same time as the normal shrimps in another vessel were doing so. If, however, food be thrown in by day, the blind shrimps will get up and hunt for it while the normal shrimps very rarely take any notice. Similarly, a blind prawn will remain in his place all day unless food be thrown in, but comes out and wanders at night. It is a singular fact that a prawn, though blind, will often find his way back to his proper place, and stay in it.

Both prawns, shrimps, *Stenorhynchus*, etc., find their food almost exclusively by scent, and when blind find pieces of food quite as quickly as uninjured ones. If a piece of worm be put into a small glass sphere with a hole in it, and the sphere is then sunk in the tank, the prawns, etc., will come out of their holes and find it. They do not seem to have any very accurate knowledge of the direction of a scent, but on perceiving it they begin rushing vaguely about, feeling the ground all the way with their chelæ. On finding the glass, the first comer will feel inside, pull out the worm, and skip with it to some high place. I have noticed that those which come after generally find the glass in which the worm has been as easily as the worm itself, and they will continue feeling inside in a puzzled way for some

time, showing that the scent remains after the worm is gone. (Conger, soles, and rockling, which all feed by smell and touch, will all do the same thing.)

Shrimps are much quicker at finding food than prawns. They hunt with their faces down on the ground like hounds questing, while the prawn hunts with his head held up as usual. If a piece of worm be just buried in sand, a shrimp will dig it out at once, whether blind or not. I have also seen a prawn, after much hesitation, plunge its two arms resolutely into an anemone (*Anthea*) and pull out a worm which the anemone had closed over. In like manner a blind *Stenorhynchus* or *Inachus* will perceive a piece of worm when it has been in the water a few minutes, and will then set out and find it. I have seen them hunting about when worms have been put into another tank from which water was flowing into their own vessel. There can then be no doubt that these animals find their food by scent, and it becomes difficult to determine what sort of objects they can see. It is not even certain that they can see each other. If a prawn is eating a piece of worm and another prawn finds it and takes it away, the first prawn will again begin to quest wildly as at first, and does not make for the prawn with the worm, though it may be only a few inches off. Nevertheless, it is certain that prawns at all events can perceive more than mere difference between light and darkness, for they notice a hand or even a thin stick placed between them and the light, putting out their antennæ towards it. *Stenorhynchus* also will put up its anterior pair of walking legs when a fish swims close over its head. It would appear that the eyes of these creatures are particularly sensitive to shadows. If a worm is hung by a thread in the water about eight inches from the bottom, the prawns will first hunt on the bottom as usual, and will then begin swimming about in quest, but on coming a few inches below the worm they will rise to it directly.

Though it seems probable that the sense of smell is obtained through the antennules, in shrimps at all events it is not exclusively so derived, for a shrimp with no antennules will hunt if a piece of worm is put very near it. On the other hand, the antennæ, of a prawn at least, appear to have no such power, as prawns when eagerly seeking food may be seen to touch it with their antennæ and still be unable to find it.

As is well known, certain crabs, as *Stenorhynchus*, *Inachus*, *Pisa*, and *Maia*, have the habit of fastening pieces of weed, etc., on their

backs and appendages until they are almost indistinguishable from the surrounding weeds if there are any. In the case of *Stenorhynchus* and *Inachus* I have often watched this process. The crab takes a piece of weed in his two chelæ, and neither snatching nor biting it, deliberately tears it across as a man tears paper with his hands. He then puts one end of it into his mouth, and, after chewing it up, presumably to soften it, takes it out in the chelæ and rubs it firmly on his head or legs until it is caught by the peculiar curved hairs which cover them. If the piece of weed is not caught by the hairs, the crab puts it back in his mouth and chews it up again. The whole proceeding is most human and purposeful. Many substances as hydroids, sponges, Polyzoa, and weeds of many kinds and colours are thus used, but these various substances are nearly always symmetrically placed on corresponding parts of the body, and particularly long plume-like pieces are fixed on the head, sticking up from it. It may be supposed that these actions are of use for purposes of concealment, and hence it might be expected that they should be dependent on the power of vision, but not only are all these complicated processes gone through at night as well as by day, but a *Stenorhynchus* if cleaned and deprived of sight will *immediately* begin to clothe itself again with the same care and precision as before. It may be mentioned that there is certainly no disposition on the part of a *Stenorhynchus* dressed in any colour, say green, to take up a position amongst green weed or indeed amongst weed at all, and so on, while some individuals which have taken up their station among weeds do not dress themselves at all.

Sense of Touch in the Rockling (*Motella*). Both the large three-bearded rockling and the small five-bearded form flourish in the tanks. They are nocturnal in their habits, and lie still all day. If a worm be thrown in by day, the small species will sometimes swim straight up and take it, having to some extent the power of seeing objects, but the large species never does this. Generally, both the animals take no notice of food thrown in until it has lain in the water some minutes, when they start off in search of it. The rockling searches by setting its filamentous pelvic fins at right angles to the body, and then swimming about feeling with them. If the fins touch a piece of fish or other soft body, the rockling turns its head round and snaps it up with great quickness. It will even turn round and examine uneatable substances, as glass, etc., which come in contact with its fins, and which presumably seem to it to require

explanation. The rocklings have great powers of scent and will set off in search of meat hidden in a bottle sunk in the water. Moreover, a blind rockling will hunt for its food and find it as easily as an uninjured one.

The barbels of the rocklings bear sense-organs having the structure of taste-bulbs, but the sensitive rays of the pelvic fins do not, having an epithelium made of tall, thin cells, somewhat like that upon the fingers of a gurnard.

Sudden Colour Changes in Conger. During the months of May, June, and July I occasionally saw the conger living in the tanks more or less covered with bright, white spots. These spots come and go suddenly, and their size varies from that of small shot to that of a threepenny-piece. Sometimes the head, both sides of the pectoral and dorsal fins, and anterior end are thus covered, while sometimes it is the posterior end or the middle of the body which is affected. I have seen these spots vanish suddenly, but sometimes they remain for several hours. It does not seem that these appearances are of the nature of secondary sexual characters, for they appear on conger of all sizes. These spots are, of course, caused by contraction of the chromatophores in the skin, but they do not appear to be connected with light, for they not only are occasional in their occurrence but once they appeared on a blind conger also. They do not appear to indicate any special emotion or diseased state, as frequently the animals thus affected are seen to feed like the rest.

Contractility of the Iris in Fishes and Cephalopods. While in warm-blooded animals the size of the pupil is regulated by the accommodatory mechanism of the iris, this power appears to be wanting amongst Teleostean fishes in general. I have examined the eyes of conger, soles, mullet, wrasse, pollock, etc., and have never seen any alteration in the width of the pupil either by day or night or in twilight, neither do they contract when a strong light is flashed on them by night. On the other hand, all the Elasmobranchs living in the tanks are provided with a means of altering the size of the pupil. In the skate this takes the form of the well-known fern-shaped process from the upper edge of the iris which by day covers the whole pupil. This structure has often been described, but I have found no mention of the fact that it is gradually drawn up in twilight and completely so at night, leaving the pupil clear. If a bull's-eye lantern be turned on to one eye, this process very slowly descends again, and in about fifteen or twenty minutes it will reach down over half the pupil. Probably if the exposure to light were continued it would fall

into the position which it occupies by day, but the skate always swam off after about twenty minutes. When the animal turned round, it could be seen that the process of the eye on the dark side had also descended to the same degree as on the light side.

In the dog-fish, nurse and angel-fish, the pupil is almost completely closed during the day by the iris, the edges of which nearly meet along a slit-shaped opening which extends more or less diagonally from the upper posterior edge to the lower anterior one. This slit gradually opens as twilight comes on and in the night the whole of the pupil is exposed. When the light of the lantern was turned into one eye of a dog-fish or nurse, the iris very slowly contracted until the edges met as by day. When the animal turned round the other pupil was seen to be still open widely as before.

The turbot[1] is the only bony fish in which any great change in size of the pupil was seen. This fish has by day a downward process of the iris, which covers the upper half of the pupil but which is drawn up at night. This process gradually returns to its position if an artificial light be shown. I have, however, also seen that the pupil of the gurnard (*Trigla cuculus*) which is almost diamond-shaped by day, enlarges somewhat and becomes circular at night.

It is difficult to correlate this power of contracting the iris among fishes with any special feature in the powers of vision or even with nocturnal habits. The skate and dog-fish in the tanks move very little by day and seem to find their food entirely by touch and smell, while the angels remain completely buried until night.

On the other hand, in such typically nocturnal fish as conger and soles there is no such mechanism of accommodation. It may be mentioned that the turbot sees very well by day and will rise to catch food falling in the water.

The eyes of the Elasmobranchs glow in the light of the lantern like a cat's eye, but the eyes of the other fishes in the tanks do not.

The iris of Cephalopods (*Eledone* and *Sepiola*) contracts for light like that of a warm-blooded animal, leaving a slit-like pupil. The size of the pupil in *Eledone* varies also with the emotions of the animal. I found that it contracted more for green light than for yellow and least of all for red. In the tanks the Sepiolas sit on the ground with their eyes closed by the lower lids throughout the day.

Modes in which Fish are affected by Artificial Light. If the fish in

[1] I have since seen the same changes in the pupil of the brill.

the tanks are looked at by night with a lantern several somewhat interesting phenomena may be seen. Fish are differently affected according as they are day or night feeders. Soles and rockling stop swimming if a light is shown, and the former bury themselves almost at once. Bass, pollock, mullet, and bream generally get quickly away at first, but if they can be induced to look steadily at the light with both eyes they gradually sink to the bottom of the tank, and on touching the bottom commonly swim away. Sometimes the fish will lie close to the glass, turning one eye only to the light; in this case the animal never lies horizontally, but always with that side of the head depressed which is turned towards the light. In this connection I may mention that I have seen a whiting which had lost one eye by disease which always swam with the blind side higher than the normal one. In the case of mullet effects apparently of a mesmeric character sometimes occur, for a mullet which has sunk to the bottom as described will sometimes lie there quite still for a considerable time. At other times it will slowly rise in the water until it floats with its dorsal fin out of the water, as though paralysed. I once saw one which remained in this odd position for some minutes after the light had been turned off it. I could not get the mullet to attend to the lamp if the room was generally lit up. The red gurnard and the bass will sometimes swim up to and lie by the light for a time, but they were never seen to take any other notice of it. Turbot, on the contrary, are occasionally greatly affected by the light of a lantern. When the light is first shown they generally take no notice of it, but after about a quarter of an hour I have three times seen a turbot swim up, and lie looking into the lamp steadily. It then seemed to be seized with an irresistible impulse like that of a moth to a candle, and threw itself open-mouthed at the lamp. On one occasion a turbot continued to dash itself with such violence at the lamp that it wore the skin of its chin through till it bled. When the light was moved to another part of the glass the turbot soon followed and began again.

Sound heard by a Lamellibranch (*Anomia*). In the course of an attempt to find out what class of sounds are generally transmitted to animals living in water I found that *Anomia* if open can be made to shut its shell by smearing the finger on the glass of the tank so as to make a creaking sound. The animals shut themselves thus when the object on which they were fixed was hung in the water by a thread. It is therefore clear that the action perceived was not

communicated merely by the jarring of the solid framework of the tank. The noise made by the finger had to be of a particular pitch, for neither mere rubbing on the glass nor the exceedingly high note made by squeezing the edge of a wet cork along the glass produced any effect. It is remarkable that the *Anomia* took no apparent notice of the sound made by creaking the antenna of a crayfish under water. Instances of real sounds being perceived by aquatic animals are so rare that this fact seemed worth recording.

THE SENSE-ORGANS AND PERCEPTIONS OF FISHES; WITH REMARKS ON THE SUPPLY OF BAIT

[*Journ. Marine Biol. Ass.*, N.S., I, 1890]

(With Plate II)

THE Council of the Marine Biological Association appointed me, in 1889[1], to make observations on the perceptions of fishes, and especially on those which constitute the modes by which they hunt for and recognise their food. It was suggested that this subject should be treated in as wide a manner as possible, and in accordance with this suggestion I have endeavoured to utilize any opportunities which presented themselves of getting an insight into the natural history of marine animals. In addition to this I have also made some experiments towards the practical solution of the bait question, both by making artificial baits, and by endeavouring to preserve materials which are already in use for bait.

The first part of this paper contains an account of those observations which seem to have a scientific interest; and it is followed by some remarks on the present condition of the supply of bait, together with suggestions as to possible solutions of the difficulty.

Evidence bearing on the perceptions of aquatic animals is somewhat difficult to obtain, owing to the absence of any points of similarity between the conditions of their lives and those of terrestrial forms. To interpret their behaviour by comparison with our own is even more clearly an inadequate treatment than it is in the case of the other lower animals. From the nature of the case, moreover, satisfactory evidence as to their conduct in the wild state is scarcely to be had, so that it is necessary to depend largely upon observations made upon them while living in tanks. It must be understood, therefore, that the statements here made are, strictly speaking, descriptive only of their habits under these artificial conditions. Though the majority of the fishes observed by me, being inhabitants of water of moderate depth, may be assumed to be under approximately natural conditions, it is important to bear this reservation in mind in considering the case of conger and other fishes which live in deeper water, and are exposed in the sea to very different influences, especially as regards pressure and light. As an instance of the need

[1] This appointment was made in connection with Mr Robert Bayly's grant to the Association for an investigation of the means whereby deep-sea fishermen may be better supplied with bait.

for caution in estimating the powers of fishes by their behaviour in tanks, it may be mentioned that the whiting, though a diurnal feeder, and apparently unable to find its food otherwise than by sight, is nevertheless under exceptional circumstances caught in the sea with a bait on dark nights at a considerable depth.

It will perhaps be convenient to give a general account of the sense-organs of the animals before describing their habits and modes of perception.

The Structure of the Sense-organs

In examining the sense-organs of fishes I have been a good deal struck with a general fact concerning them, which, though sufficiently well known and obvious when stated, does not appear to be a matter of *a priori* necessity, and it may be well to call attention to it in this place. On comparing individual fishes of the same species but of different sizes, it is apparent that the size of the eyes varies with the size of the body. The same fact is true of the scales covering the body, which seem not to increase in number, but in size as the animal grows. In fact, so constant is the number of the scales that, as is well known, they have value as characters for the purposes of classification. In the case of the olfactory organs, increase in size takes place both by growth of the individual folds bearing the epithelium, and by the addition of new folds. Now the relation of such an organ as the eye to the organism may be compared to that of an instrument to a workman; and if this comparison is a true one, it is not a little remarkable that the sizes of the two should vary together. The question next arises, is a large eye, *cæteris paribus*, more efficient than a small one? It may easily be believed that a larger olfactory organ is more efficient, but such a case as that of the eye seems more difficult. If this question should be answered in the negative, it would be interesting to see if these facts are in harmony with the principle of economy of growth, in obedience to which it is believed that all superfluous parts tend to be eliminated from the body. If it is held by any to be manifest that a larger organ is obviously more efficient by reason of its greater size, it may be asked to what limit it is proposed to carry this principle. Is it applicable to all organs and parts of organs? Are the cells, for instance, of the tissues of a large individual larger than the similar cells in a smaller one, or would they be more efficient if they were? It would in any case be most desirable to know in what animals this

relation of size between the whole and the parts is found, and to what organs it extends. In particular, it would be of the highest interest to know whether the eggs of a large individual are larger or more numerous than those of a smaller individual of the same species, and so on. An insufficient experience of Crustacea, fishes, and plants leads one to think that in these cases the number of eggs or seeds increases without change of size, though in the absence of more data it is unprofitable to discuss the matter. But as the relation between the size of the body and that of its organs has a high importance in any attempt to obtain a view of the modes of occurrence of variations, these facts in the structure of fishes are emphasised here, in the hope that persons who have the opportunity of handling large numbers of animals may be led to record their observations of similar particulars.

Eyes

The general structure of the eyes of fishes is well known, but some points which have been observed in the course of this investigation may be worthy of notice. Particular attention was paid to the eyes of those fishes which are active at night, in order to see if there is any general common feature among them. The statement, for example, is made by Day (*British Fishes*, vol. I, p. xxviii) that "nocturnal fishes require larger eyes than diurnal ones." This may possibly be true, but it is by no means the fact that they are as a rule endowed with larger eyes, as is suggested in the passage quoted. The most typically nocturnal fishes are the conger and the eel. Of these the conger has a large eye, but not a remarkably large one when compared with that of the cod or the bream, which are diurnal, while the eel has a somewhat small eye. The eyes also of the sole, which is emphatically a nocturnal animal, are singularly small, while those of the angel-fish and torpedo are still smaller in proportion to the bulk. Among the rocklings, also night-feeders, the three-bearded rockling has an eye of average size, while that of the five-bearded rockling is decidedly small in proportion to its body. Under these circumstances any general statement is misleading.

Not even is there any uniformity with regard to the presence or absence of a contractile iris amongst nocturnal or diurnal fishes. In this *Journal* (N.S., I, 2, p. 215)[1] I have given some account of my experience in this matter, which it may be convenient to repeat here, with the addition of other facts since noticed.

[1] [Cf. p. 75 *supra*. Ed.]

In the great majority of fishes observed, the shape and size of the pupil do not alter materially for light. Of the exceptions in which such a mechanism is found, some are nocturnal, as the skate and rough dog-fish, while others are diurnal animals, as the turbot. All of the Elasmobranchs which came under my notice are provided with a contractile iris, but the mode of contraction and the form of the pupil differ greatly among them. The eye of the torpedo (*T. marmorata*) presents the simplest form of this mechanism. In it the pupil is circular by night, but by day the *lower* limb of the iris rises up so as to close the pupil almost completely, leaving a horizontal slit at the upper part of the eye (*v.* Pl. II, fig. 8). In the rough dog-fish, the angel-fish, and the nursehound the pupil is also closed by day, but in it the edges of the iris meet to form an oblique slit passing across from the upper posterior margin of the iris to the lower anterior one. The arrangement in the skate is altogether peculiar, and seems to have no relation to either of these types of mechanism. In it the pupil is covered in daylight by a process of the *upper* limb of the iris, which falls over it, forming the well-known fern-shaped structure (*v.* Pl. II, figs. 7*a* and 7*b*). This peculiar iridal fold seems to consist of a constant number (eleven) of processes. By night this fold is completely drawn up, leaving the pupil clear. As described in the place referred to, the pupils of the dog-fish and skate contract at night when the light of a lantern is turned on the eye, but this contraction is not sudden, as it is in terrestrial animals and Cephalopods, but, on the contrary, takes a long time to be completed. In the skate the process of the iris did not completely descend when the eye had been exposed to light for about twenty minutes, but the pupil of the dog-fish was almost entirely closed in that time. Illumination of one eye only in the skate causes the iridal fold of both sides to descend simultaneously, but the pupil of the dog-fish remained open on the dark side when the folds of the iris had nearly met in the illuminated eye.

The eye of the sterlet (*Acipenser*), a night-feeder, also has a contractile iris, which is arranged as a circle which is incomplete at the upper edge (*v.* Pl. II, fig. 10).

Among diurnal fishes, the turbot and brill, together with the weever, all have a semicircular flap from the upper edge of the iris which partially covers the pupil by day, but is almost entirely retracted at night, slowly returning under the light of a lantern. In the Brighton Aquarium I saw a turbot in which this flap of the

iris was hardly developed at all. In speaking of the weever as a diurnal fish it is not intended to assert that it is not active at night. As is well known, it lives buried in the sand by day, but it has eyes which see well in daylight, for it will uncover itself and swim up to food just as a plaice does. As to its habits at night I have no evidence.

The pupil of the halibut is kidney-shaped, the concavity being upwards. The pupil of the plaice is of the same pattern, and without special iridal mechanism.

The pupil of the gurnard differs from all these in being slightly contracted by day so as to have a diamond shape, while it is circular by night.

All the fishes attainable were tested with a lantern by night, but in none was any alteration in the size of the pupil observed except in the cases mentioned. It is a somewhat remarkable fact that the reflex contractility of the iris, which is such a general character of land Vertebrata, should be so irregularly developed among fishes. In none of them does the usual sudden contraction for light occur, though it is nevertheless found in the Cephalopods (*v. loc. cit.*). Moreover, as the matter may have a bearing on the optical aspects of aquatic vision, attention is called to the fact that none of the animals mentioned which are provided with appliances for contracting the pupil have the circular aperture which is usual in many terrestrial animals and also in several of the other fishes which have no special mechanism of this kind.

The eyes of the three-bearded rockling (night-feeder) are extraordinarily convex, and protrude from the general level of the face so much that the lens can be seen through the cornea on looking down on the animal's head from the dorsal side. The same is true of the eyes of the boar-fish (*Capros aper*), which is a day-feeder; while those of the conger, also a night-feeder, are particularly flat.

The eyes of fishes are mostly not capable of much rotation, but those of the dory, wrasses, lump-sucker, and pipe-fishes can all be moved, and are used independently of each other (cf. p. 97). The eyes of the loach are also moveable, but to a less extent.

Olfactory Organs

In all the fishes examined olfactory organs are present, but their development differs greatly in the different forms, the largest occurring in the eel, the conger, the *Raiidæ*, and the dog-fish, and the smallest in the top-knot (*Zeugopterus punctatus*). It might be

expected that the olfactory organs of fishes which hunt by scent would be consistently larger than in those which seek food by sight, but this is only partially true. For though the great development of these parts in the eel, conger, and Elasmobranchs is accompanied by an acute sense of smell, yet in the rocklings, the loach, and the sole, which also seek their food by scent, the olfactory organs cannot be said to be proportionally more developed than they are in forms which feed by sight, such as the plaice and the pollack.

Nostrils. In all forms (? *Zeugopterus punctatus*) examined, two nostrils occur on each side in the manner characteristic of most fishes. Of these two nostrils the anterior is to some extent tubular in all the fishes (except the Elasmobranchs) which seek their food by scent (*v.* p. 90). This tube is most developed in the conger, in which it is simple and straight, projecting beyond the surface of the nose. In the eel this anterior portion of the nostril is formed of two flaps of skin. In the rocklings it takes the form of a very short tube, the dorsal edge of which is produced into a long barbel. The anterior nostril of the loaches resembles that of the rockling, but the tube stands up more vertically from the head, and the posterior edge of the aperture is not produced into a barbel, but is bent over it to form a kind of hood. This latter form of nostril is also found in nearly the same shape in *Lepadogaster*. In all these forms the posterior nostril is a simple opening without a valve.

These tubular nostrils are ciliated as well as the olfactory epithelium itself, and a current is thus caused which enters by the anterior and leaves by the posterior opening. In the majority of fishes rhythmical oscillations of the water in the olfactory pits also occur, but these are not present in any of the animals mentioned below as seeking food by scent, except *Lepadogaster*.

In the ordinary round fishes (*Gadidæ*, *Labridæ*, etc.) the two nostrils are placed close together. Through these openings currents are no doubt caused by the cilia on the olfactory organs themselves, but the principal movement of water in the olfactory chambers is an oscillatory movement which occurs rhythmically, keeping time with and being probably dependent on the respiratory movements of the fish. The former movements may nevertheless be suspended while the respiratory movements continue. It did not appear that in these fishes the water entered or left by either nostril in particular, but rather that it oscillated in and out through both of them at once.

In the flat-fishes the arrangement of this current is more complicated. The plaice may be described as having the structure which is found in most of them. This fish lies on its left side. The anterior nostrils are tubular, that of the right side being produced considerably. The posterior nostril of the right side is valvular, and opens outwards. On inspiration water passes into the olfactory chamber through the anterior nostril, and on expiration the posterior nostril opens suddenly as the water passes out through it. The posterior nostril of the left side is not valvular, but simple. These remarks apply also to the dab and the flounder. In all these fishes the nostrils are so arranged that none of them are on the *lower* surface of the head, but rather on its dorsal side.

The sole has a different mechanism. It lies on its left side, and both the nostrils of the left side are on the under surface of the head —touching the ground, in fact, when the animal is at rest. On the left side the anterior nostril is large and open, and has a ciliated fold of skin which passes spirally down it; but the posterior one is very inconspicuous and valvular, being at some distance from the anterior opening. As the sole inspires, water passes in at the anterior opening, and on expiration it leaves by the posterior nostril, which opens and shuts with a jerk. The anterior nostril of the right side is tubular, and the posterior one is valved, acting like that of the left side.

In all these fishes, also, the flow of water through the olfactory organs may be suspended though the respiratory movements continue.

In the turbot, which lies on its right side, the left anterior nostril is guarded by a simple triangular flap of skin which projects forward from the posterior edge of the opening and covers it. This possibly forms a valve during life, though I have not had an opportunity of closely examining the currents through the olfactory chamber in a living specimen. The posterior edge of the anterior nostril on the left side is produced into a very large, leaf-like flap of skin, which in dead specimens usually covers the nostril. In one specimen (from Grimsby), however, this fold was reflexed, and lay against the side of the head in such a rigid manner that it could not have been used during life to cover the nostril.

The right posterior nostril of the turbot is widely open, and the left posterior nostril is also without any special valve, but the skin at its edges nearly meets across the opening. These structures do not materially differ in the brill (*R. levis*). In one brill (from Grimsby)

the two nostrils of the right side were united, forming a common fossa in which the olfactory organ lay. In this specimen the leaf-like fold of skin, usually covering the anterior nostril, was divided into two parts, which were disposed on either side of this fossa. There was no indication that this variation was not congenital.

The left anterior nostril of *Arnoglossus laterna* is somewhat tubular, but the left nostrils of *Arnoglossus megastoma*, which also lies on its right side, were, in a preserved specimen, without valves or flaps of skin of any kind. The right anterior nostril, however, has a very large loose flap of skin. The olfactory folds are but slightly developed, and are mere ridges on the floor of the olfactory chamber. Their number in the left organ of a large specimen was thirty (*v.* Pl. II, fig. 3).

The olfactory structures of Müller's top-knot (*Zeugopterus punctatus*) are so abnormal and reduced that it will be best to reserve any statement about them until the homologies of the parts are more clear.

The *olfactory organs* themselves in fishes are composed of the well-known folds bearing the sensory and supporting cells of the epithelium. On this occasion I propose to give an account of the general structure of these organs, deferring the description of the histology until a full comparison can be made between the olfactory elements of the fishes which hunt by scent with the same parts in those which seem not to use their olfactory organs for this purpose.

The arrangement of the olfactory folds differs in the various fishes. Roughly speaking, they are built up on one of four types, or on some plan intermediate between them.

(1) In the skate and dog-fish the plates are arranged in a radiating manner on the inside of a hollow capsule, like the septa of an orange. In this case the free internal edges of the plates do not bear sensory cells, but are fibrous supporting tissues.

(2) The conger and eel have the plates of the organ arranged in two rows on each side of a central raphe, upon which the two rows are folded longitudinally so as to form the lining of the olfactory tube. The olfactory organ of the sole, though a much less considerable structure, is arranged on a similar plan; for on it the longitudinal raphe is depressed so as to form a groove from which the plates rise up on each side. The number of plates in an eel one and a half feet long was about thirty-eight pairs in each organ. As already mentioned, the number and size of these plates increase with the growth of the animal.

(3) The third type of olfactory organ, of which the second is a modification, is that most commonly found among fishes. In it the plates are fitted together in a radiating manner, forming a convex eminence in the olfactory chamber. The whole organ is either circular (as in *Cottus* and *Motella mustela*) or elliptical (as in the mackerel), according to the number and shape of the plates of which it is composed.

In all the Teleosteans hitherto mentioned most of the plates are placed at right angles to the long axis of the body, and each organ essentially consists of two rows of such plates united in the middle; for the circular collection of radiating plates of *Cottus*, etc., only differs in degree from the more common elliptical one.

Amongst the flat-fishes this elliptical series of plates arranged along a single axis is found in the genera *Rhombus* (turbot and brill) and *Arnoglossus* (merry sole and megrim). In a very large turbot the number of chief folds was thirty.

(4) In all the species of *Pleuronectes*[1] examined, as well as in *Hippoglossus vulgaris* (the halibut), an entirely different arrangement is found. In these fishes (*v.* Pl. II, fig. 2) only one row of olfactory plates is present. The plates thus arranged in a single series lie in a direction parallel to the long axis of the body, and not transversely to it, as the majority of them do in other types. The arrangement in *Solea* has already been described.

In the pollack and rockling, and probably in all fishes, if the whole olfactory organ be destroyed with acid, the skin heals over the part, but the special epithelium and the nostrils are not reproduced; but in a conger in which the olfactory organ had been only partially destroyed, the plates of epithelium were found to be regenerating from the edges of the olfactory tissue which had remained undestroyed.

Sense-organs of the Mouth and Skin

The scales and skin generally of fishes are supplied with remarkable sense-organs, which resemble the taste-buds of higher forms. These organs have been fully described and figured by Merkel in his monograph, *Ueber die Endigungen der sensiblen Nerven in der Haut der Wirbelthiere* (Rostock, 1880). In the course of these investigations a good deal of the ground covered by Merkel's work has been gone over, and to it there is little to add. It will be profitable, however, to

[1] Viz. *P. platessa* (the plaice), *P. flesus* (the flounder), *P. limanda* (the dab), *P. microcephalus* (the lemon sole of the east-coast fisheries).

mention those facts which specially concern the purposes of the present inquiry, and to describe the characters of some of these organs in forms which have not been investigated by Merkel.

Such organs consist essentially of clusters of long cells arranged together to form a bulb-shaped body, of which the apex is not covered by cuticle, but projects on the surface of the skin. The base of the bulb may be in contact with the basement-membrane of the skin, or may be separated from it by several layers of cells of the lower layer of the skin (cf. Pl. II, figs. 13 and 14). Into this base a nerve enters. Such an organ may be large and visible to the naked eye, as in the pharyngeal walls of most fishes, or it may consist of only a few such cells and be extremely minute. These minute "taste-buds" are found in clusters on the large papillæ which occur on the gill-bars of the dog-fish (as observed by Merkel), of *Cottus*, and many other forms. The whole sense-organ may be placed on the general surface of the skin, or it may be depressed into a pit or elevated on a papilla, according to its situation and the animal in question.

The cells forming these sense-organs consist of a very long, narrow cylindrical head, which is external, an internal enlargement in which the nucleus lies, and a tail passing into a fibre of varying length (*v.* Pl. II, fig. 15).

These sense-organs have a general resemblance to those of the lateral line, but the cells of which they are made do not appear to bear a hair on their peripheral buds, as those of the lateral line do.

I have examined them in the following forms, and have found them on the parts stated.

Bream (*Pagellus centrodontus*). On the palate.

Bullhead (*Cottus scorpius*). On the palate and on the papillæ of the gill-bars.

Gurnards (*Trigla*). On the palate and *not* on the fingers of the pectoral fin.

Pogge (*Agonus cataphractus*). On the villiform tentacles beneath the head.

Wrasses (*Labridæ*). On the palate as patches of minute sense-organs surrounded by ridges of skin.

Grey mullet (*Mugil*). On the palate and in great numbers upon the fleshy thickenings in the pharynx; also in rows upon the white rugæ which form the anterior borders of these thickenings.

Pollack (*Gadus pollachius*). On the lips and palate (a few).

Pouting (*G. luscus*). On the lips, palate, barbel, and pelvic fins in great numbers.

Whiting (*G. merlangus*). On the lips and palate.

Rocklings (*Motella*). On *all* the barbels, pelvic fins[1], and palate.

Blenny (*Blennius gattorugine*). No sense-organs were found on the tree-shaped processes, which stand up from the anterior nostril and from the orbit. As these are parts which might have been expected to bear such organs, mention should be made of their absence.

Plaice (*Pleuronectes platessa*). On the palate.

Dab (*Pleuronectes limanda*). No sense-organs were seen on the palate.

Sole (*Solea vulgaris*). Contrary to the natural presumption, the villi on the lower (left) side of the head do *not* bear sense-organs, though, as Mr Cunningham informs me, such organs are found between the villi.

Conger (*Conger vulgaris*). On the outer and inner lips and palate.

Eel (*Anguilla vulgaris*). On the tongue and lips and on the skin of the tubular anterior nostril.

Dog-fish (*Scyllium canicula*). On the tongue and palate and in groups on the papillæ of the gill-bars.

Torpedo (*Torpedo marmorata*). No opportunity of dissecting this torpedo occurred, but these organs should be looked for on the papillæ bounding the spiracle of this species, in which place their occurrence would be interesting.

It is of course not suggested that these organs do not occur also on other parts of the animals named, as such structures are very generally distributed among fishes.

The nature of these structures is sufficiently shown by the figures. Upon the lips of the conger two types are found, of which the most usual is shown in Pl. II, fig. 13. The sense-organ is here seen to lie on the general surface of the skin, which is very thick. Below the sense-organ a narrow channel passes up through the whole thickness of the skin, and in this the nerve travels up to the sense-organ. The other type of sense-organ found in the same situation is precisely similar, except that it does not lie superficially but at the bottom of an open pit, depressed below the surface of the skin.

The nerve-supply of the sense-organs of the pharynx of the mullet (*Mugil*), etc., and of the barbels of the rocklings (*Motella*), etc., differs

[1] In the last number of this *Journal* I stated that the pelvic fins of the rockling bore no organs of special sense. In specimens since prepared with gold chloride they are easy to see.

from these in that the skin is not channelled for the passage of the nerves to them. On the contrary, the fibres, after leaving the nerve-trunks, *pass bodily through the basement-membrane* and amongst the cells of the skin to break up on the sense-organs (*v.* Pl. II, fig. 11).

Senses of Fishes which seek their Food by Scent

Smell. The majority of fishes seek their food chiefly if not entirely by sight, but a certain number hunt for and recognise it by the sense of smell alone, while a few species are also aided in seeking by special organs of touch. The following is a complete list of the fishes which have been observed by me to show consciousness of food which was unseen by them; and, as will be hereafter shown, there is evidence that they habitually seek it without the help of their eyes.

Protopterus annectens.
Rough dog-fish (*Scyllium canicula*).
Eel (*Anguilla vulgaris*).
Three-bearded rockling (*Motella tricirrata*).
Five-bearded rockling (*Motella mustela*).
Nursehound (*Scyllium catulus*).
Skate (*Raia batis*).
Conger (*Conger vulgaris*).
Loach (*Nemacheilus barbatula*).
? Sucker (*Lepadogaster Gouanii*).
Sole (*Solea vulgaris*).
Little sole (*Solea minuta*).
Sterlet (*Acipenser ruthenus*).

To this list may almost certainly be added the remainder of the *Raiidæ*, together with the angel-fish (*Rhina squatina*) and torpedo. Unfortunately, however, the examples of these forms living in the tanks at Plymouth have never become thoroughly at home, and still (November, 1889) take food reluctantly. In fact, the skates have for many months subsisted entirely on shrimps, and very rarely take notice of other food; but owing to the kindness of Mr Wells, the superintendent, I had an opportunity of seeing the habits of the skate under more favourable conditions at Brighton.

Of the fishes in this list the conger, rocklings, sole, and rough dog-fish were the most frequently and minutely watched.

There are many points of resemblance in the habits of the various animals mentioned above, and some general observations may be made with regard to them collectively before pointing out the special features of interest in the natural history of each. In the first place they are all more or less nocturnal animals, and (? sterlet and *Protopterus*) remain in hiding by day, many of them being furnished with special modes of concealment. For example, the conger and the rocklings live in holes in the rocks, the eel and *Protopterus* in mud,

the sucker and the loach under stones, while the sole lies completely buried in the sand, the eyeballs alone being exposed. When left to themselves they generally lie motionless until dusk, when they begin to swim about with more or less activity. If, however, while they are lying thus hidden the juice of food-substances (such as squid or pilchard) is poured into the water, they come out and feel about for a considerable time, clearly perceiving the odour. The dog-fish, conger, and eels feel for food with their noses, *Protopterus* with its pectoral and pelvic fins, the rocklings with the barbels and pelvic fins, the loach with its barbels, and the sole with the villi on the left (lower) side of its head.

None of these fishes ever start in quest of food when it is first put into the tank, but wait for an interval, doubtless until the scent has been diffused through the water. Having perceived the scent of food, they swim vaguely about and appear to seek it by examining the whole area pervaded by the scent, having seemingly no sense of the direction whence it proceeds.

Though some of these animals have undoubtedly some visual perception of objects moving in the water, yet at no time was there the slightest indication of any recognition of food-substances by sight. The process of search is equally indirect and tentative by day and by night, whether the food is exposed or hidden in an opaque vessel, whether a piece of actual food is in the water or the juice only, squeezed through a cloth, and, lastly, whether (as tested in the case of the conger and rockling) the fish be blind or not. On the other hand, if the olfactory epithelium is destroyed in the rockling or conger, the animal does not leave its hiding-place to hunt, though it seizes food placed near its face. Stones or other objects rubbed with food attract these fishes as much as food itself, and when very hungry they will snap at such uneatable substances, though they are rejected after being taken into the mouth. I saw no reason to suppose that any of these animals have the instinct of following a scent (as a prawn seems to do to some extent), though they always stop to examine bodies upon which food has lately rested. The scent of the food does not seem to remain long in the water, and apparently the scent of the surface of the food itself is dissipated or decomposed in a short time; for when, for instance, a piece of squid is not found after searching, it often happens that the fishes give up and retire, but will come out again in quest if the same piece of squid be taken out, cut in half to expose a new surface, and put back. None of the

fishes were ever seen to hunt for more than about fifteen minutes unless the scent was renewed. It is difficult to estimate the distance to which a scent can be diffused in the water, but it is likely that, in water which is not rapidly moving, its virtues are destroyed before it has been carried far. There is, I think, no reason for supposing that scents are diffused through the water otherwise than by currents. This is most easily tested by experimenting with shrimps in a large shallow vessel. The shrimps remain buried until the scent reaches them. When the water was not in motion, if food was gently dropped in, the shrimps gave no sign for an indefinite time, but on stirring the water they began to seek. The longest tank at Plymouth is about twenty feet long, and an interval of from five to ten minutes elapses before conger at one end are aware of the presence of food put in at the other.

The perceptions, then, by which these animals recognise the presence of food are clearly obtained by means of the olfactory organs, and apparently exclusively through them. I was particularly surprised to find no indication of the possession of such a function by the sense-organs of the barbels and lips, or by those of the lateral line. As has been already described, the pelvic fins and barbels of the rocklings (*Motella*) and the lips, etc., of most fishes bear great numbers of sense-organs closely comparable in structure with the taste-buds of other vertebrates. No one who has seen the mode of feeding of the rockling or pouting (*Gadus luscus*) can doubt that these organs are employed for the discrimination of food-substances; but the fact already mentioned, that the rockling in which the olfactory organs had been extirpated did not take any notice of food that was not put close to it, points to the conclusion that they are of service only in actual contact with the food itself.

Sight. In view of the fact that these fishes do not habitually recognise food by sight it would be especially interesting to determine what part in their economy is played by visual perceptions. Though nocturnal animals, they all have functional eyes, which in the conger, skates, and dog-fishes are as well developed as those of other fishes (*v.* p. 82). In the angel-fish, torpedo, and soles the eyes are, however, of small proportional size. Nevertheless, with the exception of the dog-fish and skates, in which the pupil is covered in daylight by the iris, there is nothing to suggest that there is any difference between the eyesight of these forms and that of other fishes. Positive evidence as to the class of objects which they distinguish is difficult to obtain owing to the general absence of facial or other expressions

among fishes; and it should always be remembered that the fact that animals take no notice of objects is no proof that they do not see them. For example, wrasses, mullet, and other fishes with excellent sight take no notice of a handkerchief suddenly flipped against the glass of the tank in which they are, which would scare away a terrestrial animal; but it is perfectly certain that they see the handkerchief, for they will snap at a worm hanging by a thread or sticking to the outside of the glass. Similarly they take no notice of a *straight* wire held up and waved outside the tank, but if the wire be *bent* into a sinuous curve like the body of a swimming worm they (pollack) will often dash at the glass in the attempt to seize it. It would appear, however, that fish are by no means slow at gaining knowledge of this kind. A curious instance of this occurred in the case of the rockling (*Motella tricirrata*). When I first began to observe the mode of feeding of this fish I was inclined to believe that it did not *see* worms, etc., thrown in for food. As mentioned above, it does not come towards them until they have been for some time in the water, and then, moving its head and fins, it swims wildly about until it comes in contact with the food, even though it be hanging freely in the water directly in the line of sight. But one of these fishes which has been living for some months in a shallow tank has been constantly fed by persons leaning over the top; and now when hungry not only comes up and splashes about on the surface of the water as soon as any one approaches, but will lift its head out of the water to snap at the fingers held above the surface, which it obviously sees and recognises. When last observed, however, it still did not appear to have learnt to recognise a worm swimming in the water, but only the presence of the person feeding it. When it is remembered that this fish naturally hunts by scent, the acquirement of this new instinct seems somewhat remarkable, and suggests that it is not the vision which is defective, but the power of appreciation. Being a nocturnal animal, it must be supposed to have never *seen* food, or to have seen it so rarely that it made no impression on it. These considerations suggest the possibility that these fishes may in the course of time learn to distinguish food by sight as they are now habitually fed by day.

There can be no doubt that soles also perceive objects approaching them, for they will bury themselves if a stroke at them is made with a landing net; yet they have no recognition of a worm hanging by a thread immediately over their heads, and will not take it even if it touch them, but continue to feel for it aimlessly on the bottom of the

tank, being aware of its presence by the sense of smell. Soles, eels, and rocklings, moreover, have a clear appreciation of light and darkness, being always buried or hidden by day (unless food is thrown in) but swimming freely about the tank like other fish at night. When thus swimming at large they bury or hide themselves if a light be flashed on them. Conger and loaches have some appreciation of moving objects, and occasionally snap at them, but their perceptions are extremely vague, as may be shown by watching their attempts to take a piece of food trailed through the water with a line. Their movements altogether are suggestive of a blurred perception, and perhaps it may be that their eyes are capable of distinct vision under greater pressure or in less light or at a greater distance. That greater pressure might produce an effect is very possible, but on watching their movements at night with a dark lantern, or in a tank from which the light was screened, there was no perceptible difference in their aptitude in discovering food.

None of these fishes have much apparent difficulty in avoiding obstacles, but as *large* obstacles seem to be easily avoided by the same animals when deprived of sight, it may be doubted whether this perception of obstacles is not as much obtained by general sensation, especially of currents, as it is by sight.

As to the sight of the sterlet no experiments have as yet been made.

Touch. In the rocklings, as mentioned in this *Journal* (N.S., 1, 2, p. 214)[1], the pelvic fins are developed as special tactile organs, and are used in the mode there described. By these organs they are not only able to distinguish food-substances alone, for a rockling on brushing with its pelvic fins against a piece of glass or a stone smeared with vaseline, turns and examines it, clearly remarking the peculiar feel of such surfaces.

Filamentous fins similar to those of the rocklings are found in *Protopterus annectens*, in which both the pectoral and pelvic fins have this structure. Through the courtesy of Mr Wells I was enabled to watch the mode of feeding of this fish in the Brighton Aquarium. The fins are used in a manner somewhat different from that of the rockling, which merely extends the fins at right angles to the body, and swims wildly about until they happen to touch the food. *Protopterus*, on the other hand, whips with them on the bottom of the tank until the food is struck. The tail also of this fish is, perhaps, used for seeking food, but this was not clearly established.

In connection with the sense of touch, the mode of feeding of the

[1] [Cf. p. 74 *supra*. Ed.]

soles may be fitly described. The sole feeds in a manner peculiar to itself, and unlike that of any other fishes which have come under my notice. As already stated, it remains buried by day, and generally speaking, if the sand be fine its body is completely covered. When shrimps or pieces of other food are thrown in, after an interval the soles perceive it; they then give a writhing jump or succession of jumps from the bottom of the tank, and begin to search on the ground. When searching for food the upper (right) side of the sole is nearly always covered with a coating of sand so uniform that little or none of the skin can be seen. There can, I think, be little doubt that this sand sticks to the body owing to an outpouring of mucus on the surface of the skin, which probably occurs when the smell of food is perceived, and is comparable with the watering of the mouth in ourselves[1]. This covering of sand is no doubt dusted over them by these energetic movements, but it only adheres when the sole is searching for food. At night, for example, when the soles are active, they carry no sand. The coating of sand must be pretty firmly attached, for if a sanded sole is made to swim rapidly the covering of sand remains.

In searching for food the sole creeps about on the bottom by means of the fringe of fin-rays with which its body is edged, and thus slowly moving, it raises its head upwards and sideways, and gently pats the ground at intervals, feeling the objects in its path with the peculiar villiform papillæ which cover the lower (left) side of its head and face. In this way it will examine the whole surface of the floor of the tank, stopping and going back to investigate pieces of stick, string, or other objects which it feels below its cheek. As already stated, the sole appears to be unable to find food that does not lie on the bottom, and will not succeed in finding food suspended in the water unless it be lowered so that the sole is able to cover part of it with the lower side of its head, when it seizes it at once. These remarks apply to the common sole (*Solea vulgaris*), to *Solea minuta*, and probably to all the other species, but none of these have lived in the aquarium long enough for observation.

The fact that soles are hardly ever taken with a hook is no doubt due to this manner of feeding; for the bait is not allowed to lie on the bottom except in long line fishing, which is done with large hooks

[1] At the moment when a conger lying still first perceives the smell of food, he generally shakes himself, and takes a gulping inspiration, freeing a variable quantity of mucus from the skin and pharynx, which floats up through the water, owing to small bubbles of gas which are enclosed in it.

only and on rough ground. If long lines with small gear were laid on the soft ground where the soles live, it is by no means unlikely that they would be taken. In this case it would probably be found to be the most rational way of catching soles.

The sterlet and loaches on perceiving the smell of food hunt for it with their noses and barbels on the bottom. The barbels of the sterlet do not appear to be moveable as those of the pouting, etc., are, and the specimens watched at Brighton did not shovel with their noses, but protruded their remarkable jaws, and appeared to make random bites at the bottom when food was thrown in.

The Senses of Fishes which seek their Food by Sight

The majority of fishes belong to this class. The following is a list of all the species which have been observed in the Aquarium either at Brighton or Plymouth to feed in this manner. Many others—as, for example, the *Salmonidæ* and *Scombridæ*—might have been added, but I have only given the names of those which have come under my own observation.

Bass (*Labrax lupus*).
Bream (*Pagellus centrodontus*).
Bullhead (*Cottus scorpius*).
Red gurnard (*Trigla cuculus*).
Grey gurnard (Tub) (*T. hirundo*).

Pogge (*Agonus cataphractus*).
Weever (*Trachinus vipera*).
Horse-mackerel (*Caranx trachurus*).
Herring (*Clupea harengus*).
Dory (*Zeus faber*).
Boar-fish (*Capros aper*).
Goby (*Gobius minutus*).
Dragonet (*Callionymus lyra*).
Lump-fish (*Cyclopterus lumpus*).
Blenny (*Blennius pholis*).
Gattorugine (*B. gattorugine*).
Butter-fish (*Centronotus gunnellus*).
Grey mullet (*Mugil chelo*).

Three-spined stickleback (*Gasterosteus aculeatus*).
Fifteen-spined stickleback (*G. spinachia*).
Spotted wrasse (*Labrus maculatus*).
Rainbow wrasse (*Coris julis*).
Pouting (*Gadus luscus*).
Whiting (*G. merlangus*).
Pollack (*G. pollachius*).
Cod (*G. morrhua*).
Turbot (*Rhombus maximus*).
Brill (*R. levis*).
Müller's top-knot (*Zeugopterus punctatus*).
Plaice (*Pleuronectes platessa*).
Dab (*P. limanda*).
Flounder (*P. flesus*).
Shorter pipe-fish (*Nerophis æquoreus*).
Worm pipe-fish (*N. lumbriciformis*).

Sight. The sense of sight in these fishes is developed in various degrees. In some, as in the bream (*Pagellus*), the eyes are practically fixed; while in others, as in the pipe-fishes (*Syngnathidæ*), dory (*Zeus faber*), and wrasses (*Labridæ*), the eyes are capable of considerable movement, and are used independently like those of the chameleon. None of the fishes observed appear to distinguish food (worms) at a greater horizontal distance than about four feet, and for most of them the vertical limit seemed to be about three feet; but the plaice at the bottom of the tank perceived worms when at the surface of the water, being about five feet above them. Though the distance of clear vision seems to be so small for objects in the water, many of these fish (plaice, mullet, bream) notice a man appearing on the other side of the room, distant about fifteen feet from the window of the tank. When hungry they swim up to the side of the tank and show great excitement if a person approaches. The same may be seen in the case of *Octopus* at Brighton, which, when the crowd collects in front of the tank, by its rapid and excited movements shows that it recognises the signs of approaching feeding-time[1]. The range of sight of fishes on the whole appears to be short. The sight of the wrasses (*Labridæ*) in particular is plainly adapted for vision at very close quarters; for the habit of these fishes is to search for their food by minute examination of the bottom, weeds, etc., after the manner of insectivorous birds.

None of the fish seem to get any lasting appreciation of the nature of the plate-glass wall of the tank. The same fish will again and again knock its head against the glass in trying to seize objects moving on the other side. Any small oscillating substance may attract them, such as a button dangling to a thread; and pollack (*G. pollachius*) often snap at even a curl of smoke from a pipe. After repeated

[1] In this case there is some doubt as to whether the *Octopus* does not recognise feeding-time by the help of its internal sensations. I have as yet had no opportunity for accurate experiment; but Mr Wells tells me that both the *Octopus* and conger begin to swim about at feeding-time, whether any one is at the top of the tank or not. The conger are fed on alternate days, and Mr Wells assures me that they distinguish these days, and do not get excited on the off days. On two occasions only I have watched them myself. The first was not a feeding-day, and they were not swimming about; but they certainly were actively moving to and fro on the second visit, which was one of their feeding-days, as also were the eels, which is still more surprising in view of their exceedingly nocturnal habits. So far, therefore, as my observation went, it quite bore out the statement of the superintendent. The fishes at Plymouth have not hitherto been fed with regularity, as their meals have to be arranged with a view to other experiments, so that no conclusions on this point can be drawn from them.

attempts to take food on the other side of the glass they will desist; but some of the oldest inhabitants (plaice, pollack, and bream), which have been living in the aquarium for about a year, will perseveringly try again the next time. Fishes brought newly to the aquarium injure themselves by trying to escape through the glass, and I have seen gurnard fretting themselves for hours against it when the water of the tank has been made turbid by pouring in sand, being evidently of opinion that it is a way into clearer waters. It may here be suggested that perhaps the result of the famous experiment of Möbius has been wrongly interpreted. The story runs that pike, having lived for some time in a tank separated by a glass plate from another in which small fish were living, desisted from trying to catch them, and on the glass plate being removed never attempted to do so. The suggestion is that the pike had come to believe these particular fish to be under special protection. While this may be so, it is nevertheless a fact that fish, like other animals, having grown accustomed to the presence of forms which they would naturally eat, do not molest them. On one occasion several pollack were put into the congers' tank at Plymouth, and in the morning two only remained, but these two continued undisturbed for a long period; and other similar cases have been observed. The explanation should perhaps be referred to that paradoxical instinct which is widely developed among animals of many kinds, in obedience to which they occasionally do not eat or molest those with whom they are constantly associated. It is, of course, this unexplained instinct upon which the "happy family" of the travelling showman is constructed. Probably it is closely akin to many feelings and superstitions of which we are ourselves conscious, and which have received inadequate but rational explanations.

Many of the actions of fishes are of this paradoxical character. It is a common thing, when two fish swim up to the same worm, for the foremost to retire in a nervous way, leaving the worm for the other; and this quite independently of the relative sizes of the individuals. A small cod whose gills were injured lived for some time in a tank with bream and bass. This fish rarely if ever ate anything, but always swam up for a moment to each piece of food as it was put in, and then left it. When the cod approached, the bass, though many times his size, used to fall back, and return to eat the food when the cod retired. This process would be repeated again and again, and happens so often in the case of bream and bass that it appeared almost the rule for a fish to refuse at food if another fish came up behind it.

Sticklebacks and blennies, on the other hand, snatch pieces from each others' mouths like hens; so also do eels and other fish which hunt by scent. Conger, in particular, fight lustily over their food; and though they may hesitate for some time to take a piece of food which is tainted, or a substance of otherwise doubtful scent, yet they bolt it at once if another conger or a crab begins to examine it or pull it away; afterwards, if need be, they reject it. These remarks illustrate the necessity for caution in making deductions as to the likes and dislikes of fishes from scanty observations.

It has been mentioned that various fishes differ in their powers of seeing things above or on a level with them, but far more remarkable is the difference in the degree to which they are able to see downwards. Of the fish mentioned above the following were never seen to eat food after it had fallen to the bottom of the tank: bass, bream, dory, boar-fish, lump-sucker, and pollack. The pollack are particularly interesting to watch in this connection, appearing absolutely unable to find objects which have reached the ground. It may be that their vision is such as not to admit of the perception of things below them, or it may be that the whole surface of the bottom is to them indistinct and blurred, or possibly the protruding lower jaws of these fish prevent them from picking up objects lying on the ground, but certainly they never seem to attempt it; and if they fail to catch worms, shrimps, etc., as they are falling through the water they give up at once. It is to be regretted that the majority of the fishes living at Plymouth are littoral forms, and such as are accustomed to live and feed on the bottom; for it is likely that there are many other fishes which are similarly unable to find food which is below them. It may be mentioned that, in addition to those given above, it is rarely that mullet or *small* pouting find food on the bottom. Pouting of larger size, however, use their pelvic fins for this purpose, as hereafter described. In fact, it is probably exceptional for an ordinary freely swimming fish, which hunts by sight, to seek food which is not in suspension; for nearly all those that have the power of feeding on the bottom either possess organs of touch, as the gurnard and pouting, or moveable eyes, as the wrasses and pipe-fishes, or else have the eyes peculiarly placed, as the flat-fishes and blennies.

The mode of feeding of the dory and pipe-fishes is sufficiently singular to call for special remark. These animals are both provided with transparent, vibratile membranous fins. In the dory these are caudal, anal, and pectoral, while in the pipe-fishes the pectoral and

dorsal only are thus developed. By the oscillation of these the animal approaches its prey without making any general movements, and in fact stalks it. The flattened body of the dory is most inconspicuous when seen from in front, as is that of the pipe-fishes when seen end-on. The dory feeds on small fish, working up to them in this way very slowly and with precision, like a man working up to game in open country where there is no cover. On getting within range, which is some inches from the prey, the immense protrusible jaws are shot out, and the fish is drawn back with them into the mouth. When the dory sights his prey the whole aspect of the fish changes. The curious brown markings on the body, which are at times scarcely visible, blush up and become dark. Of these the most conspicuous is a wide dark band passing down the middle of the nose and continuing between the jaws; this dark stripe gives the fish a most singular appearance when seen from in front. In the case of the pipe-fish, which feeds largely on small shrimps, the face is drawn out into the well-known pipe-like process which is gradually pushed right up to the victim, who would be alarmed and escape at the approach of a more clumsily organised fish. During this proceeding the pipe-fish frequently comes forward on its ventral surface.

None of these sight-hunting fishes while living in the tanks appear able to see their food by night, or even in twilight; worms thrown in after dark fell through the water unnoticed. It did not appear that this was due to reluctance on the part of the fish to eat by night, for on some occasions pollack took worms by night when the light of a bull's-eye was turned on them so that the fish could see them. In view of this fact it would be interesting to see if fishes would take an object made luminous with Balmain's luminous paint or otherwise. I made experiments with pieces of india-rubber and with twisted glass tubes filled with luminous paint and sealed up, but none of the fish took any notice of them. Perhaps, however, such fish as mackerel might be attracted by similar objects trailed along in the open sea by night; for so many of the animals which are preyed upon by fishes are phosphorescent that it is likely that some at least are accustomed thus to recognise them.

In view of the brilliant colours which are so common among marine animals it would be highly interesting to get some idea of the colour sense of fishes, but so far my results have been chiefly negative. In the first place I endeavoured to find out if light of any particular colour were invisible to soles and other nocturnal fish which, as

already stated, swim about in the dark, but hide themselves when a light is turned on them. My experience was that their behaviour did not appreciably differ whether the light was red, blue, or green; and in fact they (eels and soles) seemed to be conscious of and to avoid coloured light almost as much as plain light. On the other hand, the pupil of *Eledone* contracts much less for red light than for other colours; and the larvæ of the lobster, which swim *towards* a light, leave red for yellow, and yellow for green, preferring blue-green to violet and to all the coloured glasses with which they were tested. As these animals seek the light it may be supposed that the blue-green seems to them the most intense. Whether, as happened in the case of Sir John Lubbock's experiments with ants, any of these animals perceive vividly the ultra-violet rays I cannot say, as I had not the necessary appliances.

As it has been suggested that the bright colours of animals may have a protective value, which suggestion has recently been extended by Garstang (*Journ. M.B.A.*, N.S., 1, 2, p. 175) to marine animals, I endeavoured to ascertain in the case of mullet whether bright colours have any such deterrent power. The mullet in question were a shoal of small fry about one and a half inches long. They were accustomed to eat minced worms off a slate slab. Upon the slate slab I arranged a number of brightly coloured tiles, some having plain and others mottled surfaces, and the minced worm was laid on these. The tiles were dark red, white, pale blue, dark blue, and mottled greenish brown. On several occasions the food was first cleaned off the pale blue and the white tiles upon which it was most conspicuous, and next off the mottled ones. The food on the dark blue and dark red tiles generally remained the longest, but was eventually eaten. On the whole it seemed to me that the fish distinguished between the tiles, but there was nothing to suggest that they were afraid of any of them. Certainly the bright colour of the pale blue tile did not seem to trouble them. It would perhaps be worth while to make a similar experiment with some of the glass models of anemones, etc., which are now obtainable, in order to test whether the colours, *per se*, have any deterrent effect.

It has been stated above that pollack will snatch at a wire curved into the shape of a worm when it is held up outside the tank. The same wire when painted white, or bright yellow, or blue, proved equally attractive.

Smell. It was stated above that the great majority of fishes hunt

their food by sight, and there is a good deal of evidence that it is sought for by sight alone. None of the fishes mentioned on p. 96 show symptoms of interest when the juice of food-substances is put into the water. They will attempt to take worms, shrimps, pieces of fish, etc., which are lowered into the water inside a glass tube, or which are simply sticking to the glass window of the tank. When hungry they are unable to find food in the dark, while by day they will seize uneatable substances which are quickly moving in the water. This evidence goes to show that the sense of smell plays little or no part in helping them to discover their food. On the other hand, both pollack and whiting, when their first hunger is satisfied, swim under the food so as to touch it with their noses and presumably smell it; and this gesture is often performed by individuals in which the olfactory organs have been destroyed, probably by force of habit. Mullet examine food by sucking water from it, and bass, bream, etc., touch doubtful food with their lips before seizing it. Plaice, turbot, blennies, and wrasses do not seem to make any preliminary examination of the flavour before taking food into their mouths. The importance of the olfactory organs to such animals as these is therefore obscure.

The range of tastes and scents which fishes are capable of perceiving seems to be very small. Conger are equally willing to eat a piece of squid or pilchard if it is covered or smeared with spirit, trimethylamine, turpentine, iodoform, camphor spirit, cheese of various sorts, anchovy extract, or *Balanoglossus*[1], as if it had been unpolluted. On the other hand, they will refuse cooked or tainted food and food which has been soaked for a few moments in dilute acids. The same remarks apply generally to the other fishes. None of them paid the slightest heed to stones or other objects covered with any of the substances mentioned. I was particularly surprised that none of the fishes in the tanks took notice of *rogue*—the fermented roe of the cod, which has a most powerful odour, and is used with great success to attract sardines by the fishermen of Brittany —but of course none of my fish were *Clupeidæ*. It is supposed by the sardine fishermen that the odour is of great importance, and must be of the right quality. Hence it may be imagined that it does not merely attract the sardines by sight.

[1] As the disgusting smells emitted by various species of *Balanoglossus* may be thought to be protective, I tested various fishes with pieces of a single damaged specimen of *B. salmoneus* which was dredged in Plymouth Sound. It was refused by both mullet and wrasse after trial, but was eaten by a sole and by a plaice.

In this place mention should be made of the fact that some of the *Gadidæ*, which are, generally speaking, day-feeders, are sometimes taken with a bait at night. At certain times of the year this is the recognised mode of catching hake (*Merluccius vulgaris*), while occasionally whiting are so taken. In both these cases the bait is sent down about *halfway* to the bottom, and not, as usually, to within a fathom of it. I was assured by fishermen that this mode of feeding is a most exceptional thing with whiting, and is supposed to be connected with the continued prevalence of calms, for under ordinary circumstances whiting-catching is not continued after dusk. In addition to these instances it sometimes happens that *large* pollack are taken on ground-lines by night. Whether in these cases the food is found by sight or by smell there is no evidence to show, for both the pollack and the whiting living in the tanks seem unable to find food in the dark. Taken in connection with the fact that this habit of whiting is supposed to occur in fine weather, it is possible that the fish are guided by the phosphorescence either of the bait itself or of the animals carried past it by the tide. Mention should also be made of the fact that trout are often taken with a worm at night.

Touch. Of the fishes which seek their food by sight some are provided with barbels, as the pouting and the cod, while a few have special tactile organs, as the gurnards, and again the pouting. When the pouting is hungry it takes its food promptly, without hesitation, but when it has had about enough it frequently erects the barbel so that it projects forward and touches the food with it, probably thus tasting it. In the Brighton Aquarium I saw that the pelvic fins of the pouting are used just as those of the rockling are, the fish swimming with them set at right angles to the body and touching the ground, but those at Plymouth were not seen to do this. The latter are much smaller specimens, which fact may possibly account for this difference in habit.

The fingers of the pectoral fin of the gurnards are certainly used in the search for food. Although the gurnards have good sight and will swim up to a bait, they are chiefly bottom-feeders, and move about with these fingers, half walking and half swimming as they seek their food. On touching a worm with the fingers they stop and scratch it about for some moments, as though raking it out of the sand, and then suddenly turn and snap it up. Though the fingers are thus employed, the gurnards often take food off the bottom

without touching it with the fingers. I did not succeed in seeing the gurnards feed by night, but it is quite possible that they may do so.

I was surprised to find that the pogge (*Agonus cataphractus*) did not appear to use the filamentous villi of the lower side of the head for finding food. These villi are developed to a great degree, and bear sense-organs which suggest that they may be used for this purpose; but though repeatedly watched, it was never seen to seek food otherwise than by sight. Thinking that these structures might be of use to it in discovering food buried in the sand, I made some trials, but the fish never seemed to recognise the presence of the buried food.

General Sensation. The power which fishes possess of avoiding obstacles even when deprived of sight is very remarkable. For example, a bream in which the cornea has been rendered opaque, after recovery from the shock does not run into the sides of the tank, but swims round in a circle avoiding them. If a large obstacle, such as a glass plate, is put in the way, the fish avoids that also. But it would seem that this is because such an object cannot be brought into position without causing a disturbance in the water which the fish perceives. For if wire rabbit-netting or straight wires are gently lowered while the fish is at the other part of his circle, he does not avoid them on returning the first time. After colliding with such an object, though very gently, the fish seems to lose its balance, and does not swim upright for some seconds after, lying over generally towards the left side. If the wires are left in place the fish does not again run into them, but swims in a reduced circle. The sensibility of these fishes to movements in the water must be exceedingly delicate; for if a straight wire is put in the path of a blind fish it will be avoided if the finger only is kept on the top of the wire, though it does not avoid it if the wire is standing by itself. The same is true of pollack which had become blind from disease (apparently of the nature of cataract, to which fishes in captivity are very liable). It has been held by some observers that the sense-organs of the lateral line are of importance to the equilibration of the animal. Apart from the difficulties presented by the structure of these organs, which closely resemble taste-buds, it must be held that the case of the flat-fishes is practically conclusive against this view. For in the flat-fishes not only do the lateral lines retain the same position relative to the symmetry of the animal that they occupy in other fishes, but in those fishes (*e.g.* the dab, etc.) in which the course is peculiarly curved, this

curve occurs equally on the upper and under surfaces. But as the flat-fishes swim in a plane at right angles to that of ordinary fishes the two lateral lines come to lie in the same vertical planes, and can therefore hardly be supposed to assist in equilibration. The fact that a fish in which the lateral nerve has been severed is unable to swim uprightly scarcely bears on this question, for almost any severe injury upsets the equilibrium of a fish.

Shoaling. It was suggested to me by Professor Lankester that inquiry should be made as to the manner in which fishes keep together in shoals, and especially whether they follow each other by sight or otherwise. The only shoaling fish which was living in quantity in the tanks at Plymouth is the grey mullet. By day the whole shoal of about fifty little ones stays together more or less. Sometimes it divides into two or three shoals, but they run closely together if alarmed[1]. At night they lie *on the surface* of the water, and seem not to swim about as a body, nor are their heads all pointing one way as they generally are by day. The shoal seems at no time to have any leader, but will sometimes follow the front fish until one of those that are behind makes a dart elsewhere, when the whole shoal turns round and follows. They certainly have no tendency to follow the largest fish in the shoal, or indeed any fish in particular. Similarity in size seems to be usual in these shoals. In one of the tanks there are two mullet which have been there for about a year, and are now about three inches long. They live apart on the ledge of the overflow, and never consort with the other mullet, which are about six inches in length. When, however, some of this year's fish (three-quarter inch) were put in, these two immediately swam out to them, and they all retired together into the overflow channel, where they afterwards remained habitually.

To the fifty small mullet in the long tank I introduced twenty more of rather smaller size, but of the same age, which had lived in another tank. The fifty at once ceased feeding, and huddled timidly away behind the stand-pipe, where they were joined by the newcomers. After a time the latter all left them in a body, thus showing that they recognised each other in some manner. They soon returned,

[1] This instinct of packing together when afraid seems to be general among fishes which move in shoals. Mr Dunn tells me that the proverbial phrase, "as close as hakes in a hoop," is derived from the fact that such fishes huddle together when surrounded by a net. Shoals of pilchard, herring, etc., also pack together when attacked by sea-birds.

however, and after staying together for a little a detachment of the new-comers again left, and so on; but on the following day the two shoals had amalgamated and fed together. Weakly fish never swim with the shoal, but keep apart—whether by choice or compulsion could not be determined.

Two specimens of horse-mackerel (*Caranx trachurus*), about two and a half inches long, put in in September, shoaled with the mullet, but the gobies never do so. In November on returning to Plymouth I found that one of the horse-mackerel was dead, and the other had left the mullet and moved about alone, but if alarmed it at once joined the mullet.

From the fact that the mullet do not move as a shoal at night, it may be so far inferred that they follow each other by sight alone, but it would be interesting to know whether other shoal-fishes travel at night. It may, in fact, be doubted whether such fish as pilchards habitually move about as a shoal at night. Of course drift-netting is carried on at night; but the nets are shot in places where the pilchards or herrings are known to be, and possibly the slight movements of the individuals and currents may take them into the net. That the shoals under some circumstances do not travel at night is seen by the use of the method of seeking pilchards known as "briming" for them. In this operation, which I have never seen, but which has been described to me by several fishermen, as the boat sails along a man stands on the cuddy and stamps his foot at intervals. When the boat is among the pilchards, they are then seen by means of the "briming" or phosphorescence to dart away in all directions. Presumably, then, until disturbed by the noise they were lying at the top of the water, as the mullet were observed to do in the aquarium.

Hearing. Several attempts were made to determine the class of sounds which fishes can hear. During the month of November some blasting operations were carried out on the premises of the Association, and particular notice was taken of the behaviour of the fish. The pouting scattered for a moment in all directions when the report came, but were quiet directly afterwards. The soles, plaice and turbot buried themselves. The conger drew back a few inches, as is their habit also when a light is turned on them at night, and generally on being disturbed. None of the other fishes were seen to take any notice of the report.

As mentioned in this *Journal* (N.S., I, 2, p. 217)[1], satisfactory

[1] [Cf. p. 77 *supra*. Ed.]

evidence was obtained that the creaking sound made by smearing a wet finger on the glass window of the tank was heard by a Lamellibranch (*Anomia*). For some time I was of opinion that the same sound was heard by some fishes (pollack, etc.) which at once come to the spot and follow the finger. Mr Wells, of the Brighton Aquarium, told me that his own observations led him also to believe this, especially in the case of bream, which come to the front in a body when this sound is made. Nevertheless, on further trials I saw no reason to suppose that the fish were not merely following the finger by sight, and I never saw them (pollack) attracted when the sound was made behind a screen of silk or weeds sunk in the water, and such a screen would scarcely interfere with the transmission of the sound. The movements of the bream at Brighton did not, however, resemble those of fishes trying to catch a particular piece of food, but were distinctly suggestive of general expectation. Seeing that the case of the *Anomia* proves that sensible vibrations are thus actually set up in the water, it may be that they hear them. The sound made by pebbles rattling inside an opaque glass tube does not attract or alarm pollack; neither are they affected by the sharp sound made by letting a hanging stone tap against an opaque glass plate standing vertically in the water. If they *see* the stones in either of these cases they follow them, but if the glass is opaque they do not. When the wall of the tank is struck with a heavy stick they behave as described in the case of blasting. As might be expected, none of the fishes were seen to take notice of sounds made in the air. Various loud noises were tried, but soles, for instance, when exposed did not bury themselves as they do when the side of the tank is struck. Probably, therefore, they did not hear the noises. The stories, for example, quoted in Day's *British Fishes*, p. xxxviii, of fishes coming to be fed when a bell was rung, can scarcely be taken to prove that the sound of the bell was heard by them, unless it be clearly proven that the person about to feed them was hidden from their sight. The sound of the chopper which is also there mentioned in this connection may have been communicated directly by the walls of the tank. There is no reasonable doubt that in the operation of "*briming*" for pilchards (*v.* p. 106), the sound made by the stamping of the foot is actually heard.

Though it may, therefore, be regarded as clear that fishes perceive the sound of sudden shocks and concussions when they are severe, it can scarcely be supposed that sounds of this nature play much part in their ordinary life, even if they occur at all. On the other hand,

they do not seem to hear the sound of bodies moving in the water which they do not see. It may be remarked that the sounds emitted by fishes and *Crustacea* (dory, gurnard, crayfish, etc.) are of a stridulating or grumbling nature. In addition to these Mr Wells called my attention to a peculiar snapping sound (audible in the room) which is made by large wrasses when feeding and biting with their strong jaws.

Remarks on the Supply of Bait

The observations recorded above were made as a first step towards a practical solution of the difficulties which beset the bait question. It was felt that any attempt to find a cheap bait must be begun by getting a knowledge of the ways in which fishes find and recognise their food; and it was anticipated that when such knowledge should have been acquired, it would be possible to make use of it in a practical manner. Though the practical side of the subject was beyond the scope of this part of the investigation, it may be permissible to make a few remarks upon this aspect of the matter, and to indicate the lines of practical experiment to which these observations point.

The fishes which are chiefly sought by long-line fishermen on the south coast of England are conger, skates, and rays; while elsewhere the most important fishes which are taken with a hook are cod and halibut (*Hippoglossus vulgaris*). The chief substances used as bait are—for the east coast of England and North Atlantic, the herring; for the Scotch fisheries, the whelk (*Buccinum undatum*) and the mussel (*Mytilus edulis*); on the south coast of England the squid (*Loligo vulgaris*) and the pilchard are most in demand; while in the Channel Islands *Eledone* is used in great quantity. Everywhere the supply of bait is costly, and at times it fails, owing to calms or bad weather. It is therefore important that some substance should be obtained or manufactured which is attractive to fishes, but cheaper and more regularly accessible than the natural baits at present used.

In any attempt to prepare such a substance it is of the first importance to ascertain the mode by which fishes find and distinguish their food. As has been here set forth, satisfactory evidence was obtained that conger and the *Raiidæ* seek their food by smell. While I was at Plymouth no opportunity occurred of watching the habits of the cod, for only one injured specimen was obtained. It was quite clear that this fish saw exceedingly well, but whether or not the barbel or olfactory organs may not be used also in seeking food on the bottom or at night I am unable to say, but from experience of

other fishes it is *à priori* unlikely that they are of great value as organs of search. The halibut is of course not found on the south coast, and has not come under my observation in the live state; but the structure of the fish, which closely resembles the plaice, suggests that it feeds by sight. This suggestion is strongly supported by the statement of Pennant quoted in Day's *British Fishes* (II, p. 7) that on two occasions halibut had been known to take a sounding-lead. The fishes, then, which are sought by the North Sea fishermen and others differ from those upon which the Plymouth men most depend, for the former feed by sight and the latter by scent. As might be expected, therefore, the same bait is of different value in the two cases. For while in the North Sea the herring is thought to be the best bait, Plymouth fishermen scarcely think it worth their while to go to sea with it. At Plymouth, for catching conger fresh squid is thought to be the best bait, and fresh pilchard is by some considered as good as regards attractiveness, but as it has not the toughness of squid it does not stay on the hook so long. My own experience with conger in the tanks leads me to think that squid is also more attractive as a scent than pilchard is. In the absence of pilchard and squid, mackerel is used when abundant, but usually this fish is too dear to be in use as bait, and it certainly does not attract conger as much as squid.

The facts already given point to the conclusion that for the purposes of the conger and skate fishery the bait question may be solved in one of three ways: either

(1) By extracting the flavour of squid or pilchard, and compounding it with some tough substance which will not wash off the hook; or

(2) By finely dividing squid or pilchard and mixing it with some cheap substance, so as to make a little of it go further; or

(3) By preserving squid or pilchard when abundant in such a manner as not to destroy its flavour and scent: of course this last method would only help the fishermen to tide over periods of scarcity of bait.

I have made some experiments in each of these directions, and perhaps a record of my experiences may be useful to those who intend to go on with the subject.

(1) This would no doubt give the most complete solution of the whole difficulty. I made some preliminary experiments with extraction by ether, and found that both from *Nereis* and from herrings

after the ether had been distilled off, an oily fluid remained, which certainly attracted rocklings most powerfully, and caused them to snap at stones dipped in it. That obtained from herring also brought the conger out of their holes, but they did not show the eagerness that they do when seeking actual food.

Mr Bourne has prepared a remarkable fluid by simple distillation of squid and water. This has a strong smell resembling that of cooked squid, and has stood for over a year without decomposition. It did not appear, however, that the fish noticed it at all.

By adding spirit very gradually day by day to mashed squid mixed with sea water which was kept warm, a good deal of the scent was extracted, and when the conger were very hungry a few c.c. of this extract poured into the tank sufficed to put them into a state of great excitement; they would seize rags which had been dipped in it, but I did not succeed in compounding it with any substance which they cared to eat. These results, though incomplete, are so far fairly encouraging.

(2) Many attempts were made to incorporate finely divided squid with gelatine. It seemed possible that if gelatine into which mashed squid had been stirred whilst warm and liquid, could be cast into sheets and dried, it might perhaps retain its flavour sufficiently to be eaten on being again softened with water. Consistency was given to these sheets of gelatine by stretching a sheet of butter-cloth in them when warm. When the conger were *very* hungry they would eat this substance with hesitation, and in the sea I caught an occasional fish (rockling and conger) with it, but it was by no means satisfactory, probably because each particle of squid was so coated with gelatine that its scent could not get out.

The next experiment was made by pouring melted gelatine into dishes smeared with mashed squid or mackerel, and then laying sheets of tissue-paper similarly smeared on the upper surface of the gelatine before it had set. When the gelatine was cold the paper was stripped off, and the gelatine remained covered on each side with a thin smearing of fish. The fish in the tanks ate this substance when fresh as readily as ordinary food, but it is unsuited to the purposes of fishing in deep water, as the coating of fish is washed off, and no doubt soon loses its scent. Probably the difficulty arising from the fact that the scent is soon destroyed on the surface of the food would prevent its being used in a finely divided form, however compounded.

(3) In experimenting with squid on a small scale I found that it

could easily be preserved for about a month by cutting it open, cleaning and drying it with a cloth, and then powdering it with boracic acid and flour. This squid was apparently unchanged, and was in excellent condition for bait. Unfortunately, now that so many of the trawlers go away to the Bristol Channel, but little squid is landed at Plymouth.

Salted squid and salted pilchards are used, but are very unsatisfactory.

On a small scale pilchards were preserved for three weeks in the same way with boracic acid and flour, and were satisfactory as bait for conger. I succeeded also in catching mackerel at the time when they were feeding near the bottom (August and September) with preserved pilchard and preserved squid[1]. With the kind assistance of Mr Matthias Dunn, of Mevagissey, I laid down several barrels of pilchards with boracic acid and flour as described, but for some unknown reason they did not answer. Though not decomposed, in a month's time they had become what is called by fish-curers "rusty," and their scent was that of cured fish rather than that of fresh. My experience with them on a small scale leads me to believe that with experience and precautions they might be kept with boracic acid in the dry state. Of course this preservation should be made with winter fish, which contain much less oil than summer fish. There is little hope that they could be preserved for bait in a *solution* of boracic acid, from the fact already mentioned that the scent of these things seems to be destroyed by contact with water.

In conclusion, I may repeat that the experiences here given suggest that the first step to a proper solution of the bait question for the south coast and Channel Island fisheries, where *fishes which hunt by scent* are caught, must be made by the extraction of the scent of squid or pilchards. Whether an artificial bait flavoured with such an extract would be useful in the fisheries of the North Sea, etc., cannot be predicted, but if made of some bright or white material (as dough or china clay) it might probably prove equally attractive to fish which hunt by sight. At the same time it must be borne in mind that any artificial bait must be extremely cheap if it is to be preferred (in the North Sea) to herrings, which are to be had for a

[1] When mackerel are fished for at anchor with a hand-line, these two baits are used *together*, a small piece of each being put on the hook. It is difficult to explain the reason of this curious practice, but either bait alone is said to be of little use, which my own experience fully confirms as far as it goes.

great part of the year. It would, moreover, be interesting to see whether the conger, etc., of the North Sea would take pilchard or squid, which they have probably never met in their ordinary experience.

Description of Plate II

Fig. 1. Head of a dab (*Pleuronectes limanda*), nat. size, showing the position of the olfactory organ as seen when the skin is removed.
Fig. 2. Diagrammatic representation of the right olfactory organ of the dab.
Fig. 3. Outline of the face of a megrim (*Arnoglossus megastoma*), showing the left olfactory organ as seen when the skin is removed (nat. size).
Fig. 4. The olfactory plates of the left olfactory organ in a turbot (*Rhombus maximus*). The dotted circles show the position of the nostrils, and the arrows the course of the current.
Fig. 5. Diagram of a single olfactory plate in the turbot, showing the mode of attachment to the rachis.
Fig. 6. Diagram of the pupil of the rough dog-fish (*Scyllium canicula*). *a*, by day; *b*, by night.
Fig. 7. Pupil of skate (*Raia batis*). *a*, by day; *b*, by night.
Fig. 8. Eye of torpedo. *a*, by day; *b*, by night.
Fig. 9. Pupil of angel-fish (*Rhina squatina*). *a*, by day; *b*, by night.
Fig. 10. Pupil of sterlet (*Acipenser*). *a*, by day; *b*, by night.
Fig. 10A. Pupil of turbot (*Rhombus maximus*). *a*, by day; *b*, by night.
Fig. 11. Longitudinal section of skin of barbel of rockling (*Motella tricirrata*), preserved with gold chloride to show the nerve-fibres traversing the skin to supply the "taste-buds." Zeiss' obj. D, oc. 2.
Fig. 12. Horizontal section of skin of barbel of rockling (*Motella tricirrata*), to show the immense numbers of "taste-buds" which it contains. Zeiss' obj. A, oc. 2.
Fig. 13. Vertical section of skin of lip of conger, showing a "taste-bud," and the nerve running to it in a channel through the skin. Zeiss' obj. D, oc. 2.
Fig. 14. Vertical section of skin of pharynx of mullet (*Mugil*), showing a row of "taste-buds." Zeiss' obj. D, oc. 2.
Fig. 15. Cells of one of the "taste-buds" of a mullet (*Mugil*) macerated in Hertwig's fluid. Zeiss' obj. F, oc. 2.
Fig. 16. Cells of "taste-bud" of pollack (*Gadus pollachius*). Zeiss' obj. D, oc. 2.
Fig. 17. "Taste-bud" in skin of the tongue of an eel (*Anguilla vulgaris*), preserved with gold chloride to show the nerve-fibres. Zeiss' obj. D, oc. 2.

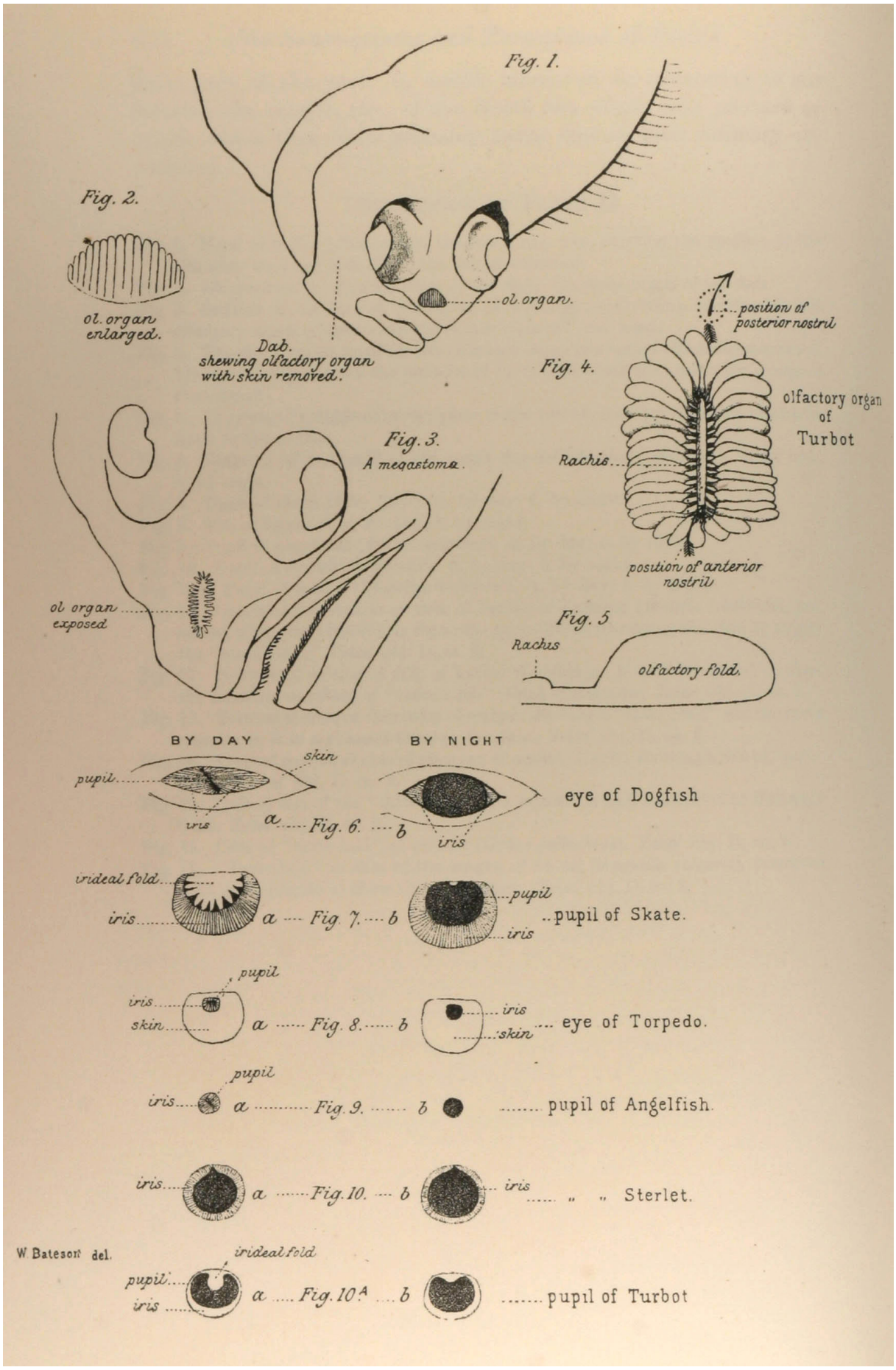


Fig. 1.
ol. organ.
Dab.
shewing olfactory organ
with skin removed.
Fig. 2.
ol. organ
enlarged.
Fig. 3.
A megastoma.
ol organ
exposed
Fig. 4.
position of
posterior nostril
olfactory organ
of
Turbot
Rachis
position of anterior
nostril
Fig. 5
Rachis
olfactory fold.
BY DAY
BY NIGHT
skin
pupil
iris
a
Fig. 6.
b
iris
eye of Dogfish
irideal fold
iris
a
Fig. 7.
b
pupil
iris
pupil of Skate.
pupil
iris
skin
a
Fig. 8.
b
iris
skin
eye of Torpedo.
pupil
iris
a
Fig. 9.
b
pupil of Angelfish.
iris
a
Fig. 10.
b
iris
" " Sterlet.
W Bateson del.
irideal fold
pupil
iris
a
Fig. 10A
b
pupil of Turbot

Fig 11.

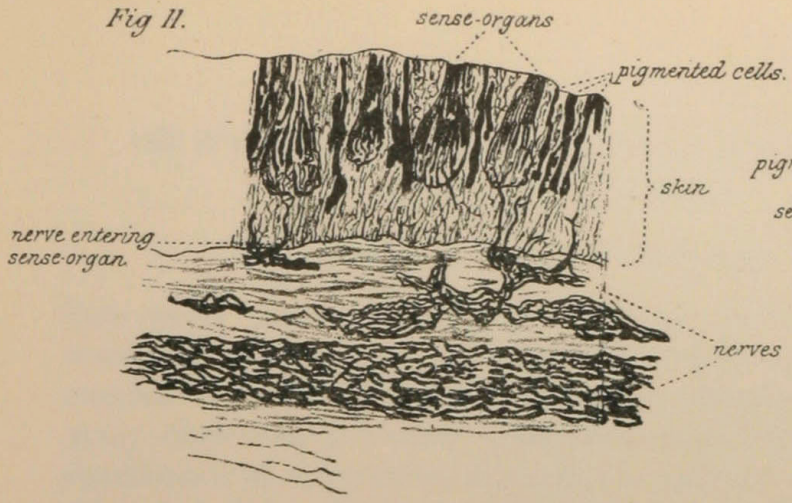


Fig. 12.

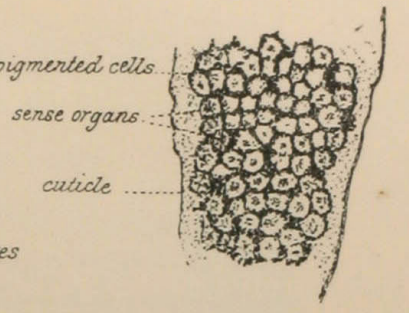


Fig. 15.

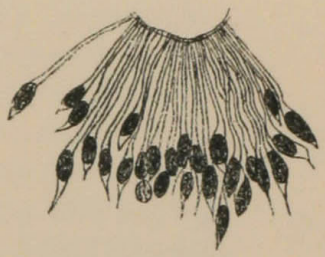


Fig. 13.

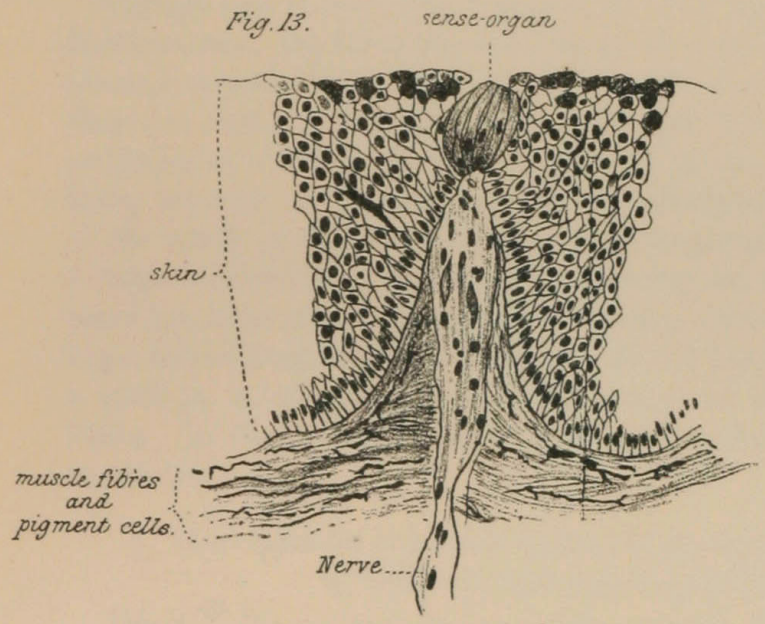


Fig. 16.

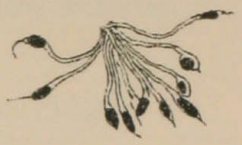


Fig. 14.

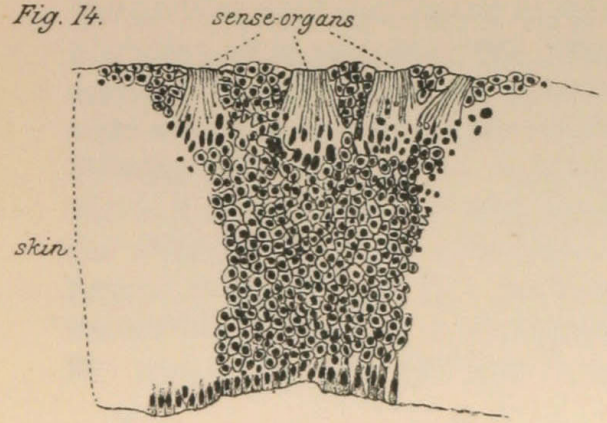
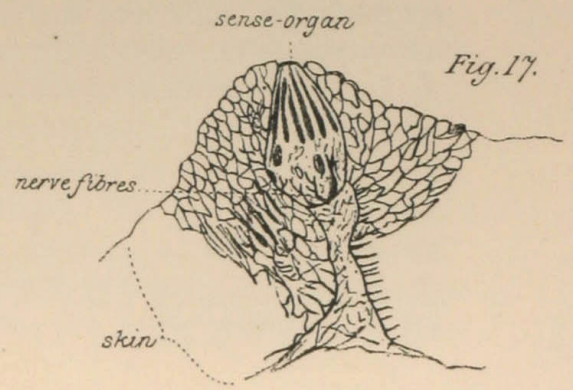


Fig. 17.



ON SOME CASES OF ABNORMAL REPETITION OF PARTS IN ANIMALS

[*Proceedings of the Zoological Society*, 1890]

THIS paper contains descriptions of some instances of variations consisting in abnormal repetitions of normal structures. A large number of similar or identical facts have already been recorded by many observers, yet every additional record is valuable; for the significance of a variation depends not only on the form which it takes, but also on the frequency and the degree of completeness with which it takes that form.

Though one is naturally tempted to draw seemingly obvious deductions from the facts about to be given, it is not proposed on the present occasion to do more than describe the actual structures as they are found. For while it is clear that the key to some of the problems of variation is to be sought by an analysis of this class of facts, yet such an analysis can only be attempted after a wide survey of the whole ground, and when it shall be possible to bring forward a large collection of the evidence bearing on the subject. I have been for some time engaged in preparing such a collection, and I hope before long to find an opportunity of putting it in order with a view to a full discussion of the modes of variation of Multiple Parts. In the meantime it is best to describe the forms without comment.

I. *Crab* (Cancer pagurus) *having the Endopodite of the Third Maxillipede represented by a Chela*

This animal was brought by a fisherman to the Laboratory of the Marine Biological Association at Plymouth. It is a male, measuring five inches from one side of the carapace to the other. All the parts appear to be normal with the exception of the third maxillipede of the right side. This structure, however, has the form shown in Fig. 1, A, differing entirely from the ordinary condition of the appendage. Fig. 1, B, is taken from the third maxillipede of the left side and shows the ordinary structure of the same parts. On comparing the two figures, it will be seen that the protopodite does not differ in the limbs of the two sides; that the exopodite of the right side is essentially like that of the left, but that it lacks the inner process and the

flagellum which are borne by the normal part. There was some indication that this branch of the limb had been injured, and perhaps the flagellum may have been torn away, but the appearances were not such as to warrant a conclusion on this point. The branchial epipodites (not shown in the figures) were normal in both cases. The endopodite of the right side was entirely peculiar and was, in fact, literally transmuted into the likeness of one of the great chelæ. It consists of a single joint (*mi*), articulating with the protopodite centrally and bearing the carpopodite. This single joint represents, as it were, the ischiopodite and meropodite of an ordinary chela, but these two parts are ankylosed together, and the articulation between them is only represented by a groove (*g*); another groove (*g'*) represents the groove upon the ischiopodite of the chela at which the

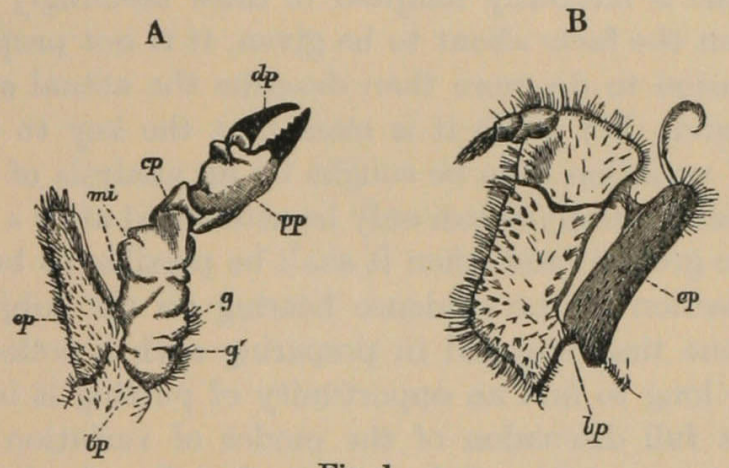


Fig. 1

A represents the abnormal third maxillipede of the right side. B shows the same parts on the left side, which are normal.

bp, protopodite; *ep*, epipodite; *dp*, dactylopodite; *pp*, propodite; *cp*, carpopodite; *mi*, meropodite and ischiopodite ankylosed together, *g* indicates the line of their separation; *g'* corresponds to the groove at which a chela can be thrown off.

limb is commonly thrown off by the animal if it is injured. The carpopodite, propodite, and dactylopodite are feebly movable on each other and hardly differ, save in absolute size, from those of the normal chela. The shape, proportions, and texture are all those of the chela.

Cases like the foregoing, of the complete transformation of a part into the likeness of another part, though very common among plants, are rare amongst animals. This variation is especially interesting from the fact that a precisely similar case of the transformation of the third maxillipede (left) into a chela has been already observed in *C. pagurus* (Cornish, T., *Zoologist* (3), VIII, p. 349).

II. *Cases of Repetition of the Pincers of the Chelæ in Crabs* (Cancer pagurus)

A and B. These two specimens were brought by fishermen to the Plymouth Laboratory. The greatest measurement of the carapace was in each case about five inches. The one specimen was a male, but the sex of the other was not noted. With the exception of the varying structures about to be described, the animals seemed normal and healthy. In A the chela of the right side had the form shown in Fig. 2, A (p. 116), which represents the limb seen from the outside. The dactylopodite bears two supernumerary, fixed processes. Whether the *outer* pair of processes which curve towards each other are the extra ones, or whether two processes have grown up on the inside of the dactylopodite, cannot be affirmed; but the latter seems more likely. If this is the true interpretation, it will be seen that one of the extra processes curves towards the "index" of the limb, while the other turns to meet the dactylopodite.

Though the fact may have no relation to the presence of this supernumerary structure on the right side, it should nevertheless be mentioned that the chela of the left side, which was otherwise perfect, had lost its dactylopodite. The socket in which the dactylopodite usually moves was filled with a plate of hard shell, but whether the joint had been lost by injury or had been congenitally absent could not be affirmed. Since mutilated limbs are generally thrown off by Crabs, the presence of such a chela without the dactylopodite is so far evidence that this joint had not been lost by an accident. As, however, according to the observations of Heineken (*Zool. Journ.* vol. IV), such mutilated parts are occasionally retained, much stress cannot be laid on this consideration.

The left chela of B is shown in the figure as seen from the inside. The dactylopodite bears a thick process which divides peripherally into two stumpy projections which bear teeth on their inner faces. These projections are like the normal pincers in consistency and colour.

C. This specimen was kindly lent to me for description by Mr J. Carter, F.R.C.S., of Cambridge. It is the right chela of a *Cancer pagurus*. In it the repetition of parts is far more extensive than in either of the preceding specimens. As is shown in Fig. 2, C, it bears two dactylopodites, each complete in all respects, and to each of these dactylopodites is opposed a fixed process. In addition to this, one

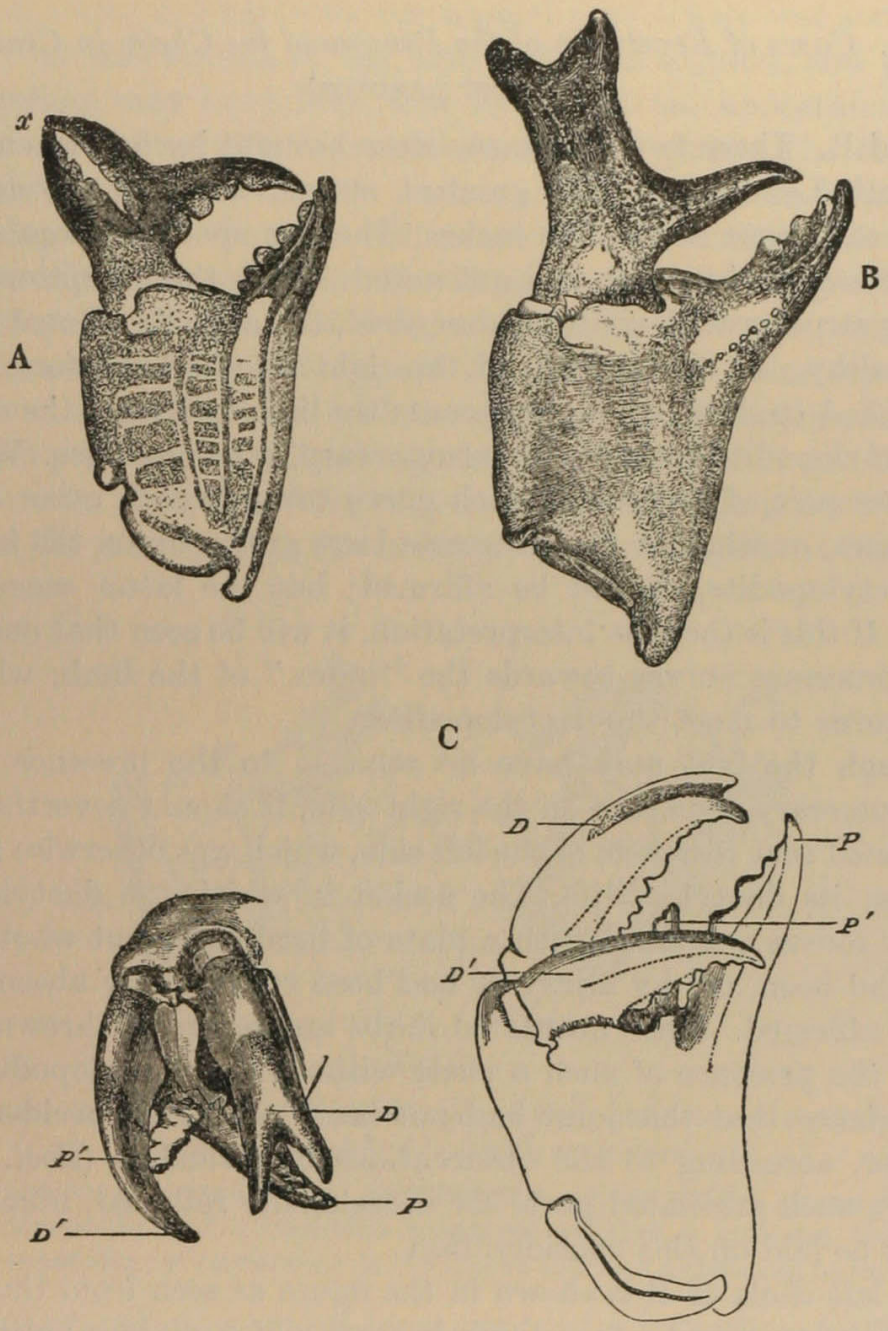


Fig. 2

Abnormal claws of *Cancer pagurus*.

A is shown from the outside; B, from the inside; C is represented as seen from the end and from the outside.

(The two processes overlap, but do not meet, at the point *x*.)

(Figures B and C were drawn for me by Miss M. J. Davidson.)

of the two dactylopodites is partially divided longitudinally into two, and at its free end terminates in a pair of toothed processes. The teeth on these processes are continued downwards on the inner

surface of the joint in two complete rows. The total number of points borne by this claw is five.

Though there is not sufficient evidence for determining the question, it may be mentioned that the general appearance suggests that the double dactylopodite, D, is the normal one of the limb and that the process, P, which is warped over to meet it, is the process normally opposed to it. The process P', which is opposed to the dactylopodite, D', is comparatively small and ill-developed.

The class of variation shown by these three specimens is not uncommon amongst Decapoda (cf. Faxon, Léger, etc.).

In addition to these cases an especially interesting one should be mentioned which was communicated to me by Mr G. C. Bourne, Director of the Marine Biological Laboratory. This specimen, which was not seen by myself, was sent to Mr Bourne by Mr Dunn of Mevagissey, Cornwall. It was an edible crab (*C. pagurus*), measuring about 2·5 inches across. In this specimen the three posterior walking-legs of one side were seen to be each repeated. It had lately moulted and was much decomposed when received. Unfortunately an imperfect examination of it was made and the specimen has been destroyed. Similar occurrences among crustacea and insects have been recorded by Léger and others.

III. *Beetle* (Chrysomela banksii) *having three complete Tarsi on one Leg*

This specimen was kindly lent to me for description by Dr Sharp, who obtained it from the New Forest.

It was exhibited at a meeting of the Entomological Society in 1862, but has not been figured or described in detail. The tibia of the third leg on the right side has the form shown in the figure. Its outer

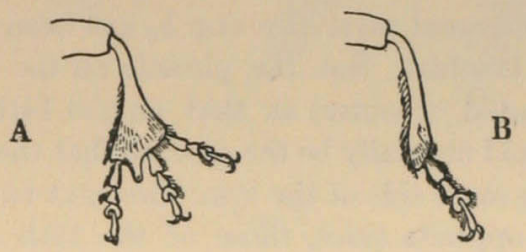


Fig. 3

A, Abnormal right posterior leg of *Chrysomela banksii*. B, Normal leg in the same position, from a rather larger specimen (enlarged to scale).

(Figures drawn by Mr Edwin Wilson.)

extremity, which is widened into a flat, club-shaped structure, bears three complete tarsi, each of which is perfect in all its four joints and carries a pair of normal claws. These three tarsi are equal in size, but are very slightly smaller than those of the same leg on the other side.

In addition to the three tarsi the tibia is produced into a small horn, which projects from it rigidly, having no articulation. At the apex of this horn is a small circular pit which is apparently closed by membrane. The other appendages are normal.

A considerable number of cases similar to the above have been collected, especially by Kraatz, Mocquerys, and Jayne.

IV. Antedon rosacea *with Abnormal Repetition of the Brachial Structures*

This individual was found amongst a number of other specimens of *A. rosacea* collected by a party that had been dredging for the Plymouth Laboratory in the Hamoaze, near Beggar's Island.

In normal individuals of this species the arms after leaving the radial plates do not again divide, but are continued to their ends as a single row of brachial plates, which bear pinnules on either side alternately. The present specimen, however, bears two arms, which, after being continued normally for a certain distance, break up into several secondary arms. The diagram (Fig. 4, A) shows the relation of these two varying arms (lettered b_2 and e_1) to the mouth and anus. It is seen, therefore, that they are *symmetrically* placed.

As I am inexperienced in the use of Crinoid terminology, I sent this specimen to Dr P. H. Carpenter, who has very kindly supplied the following description of it:

The abnormal arms of this remarkable specimen are symmetrically placed as regards the mouth and anus, being the posterior arms, b_2 and e_1, of the two anterolateral rays. The arm b_2 has been regenerated at the syzygy in its 15th brachial. But the pinnule on the new epizygal is on the same side (abradial or outer) as that on the 14th brachial, and not opposite to it as would normally be the case, so that there are two pinnules in succession on the same side of the arm. The next twelve pinnules alternate regularly on opposite sides, those of the 19th and 27th brachials having much enlarged basal joints. That on the 28th brachial is considerably larger than its predecessors and more like a bifid armlet. It commences with five large joints, the last of which bears two pinnules, the one continuing the main axis being rather stouter than its fellow. The 29th

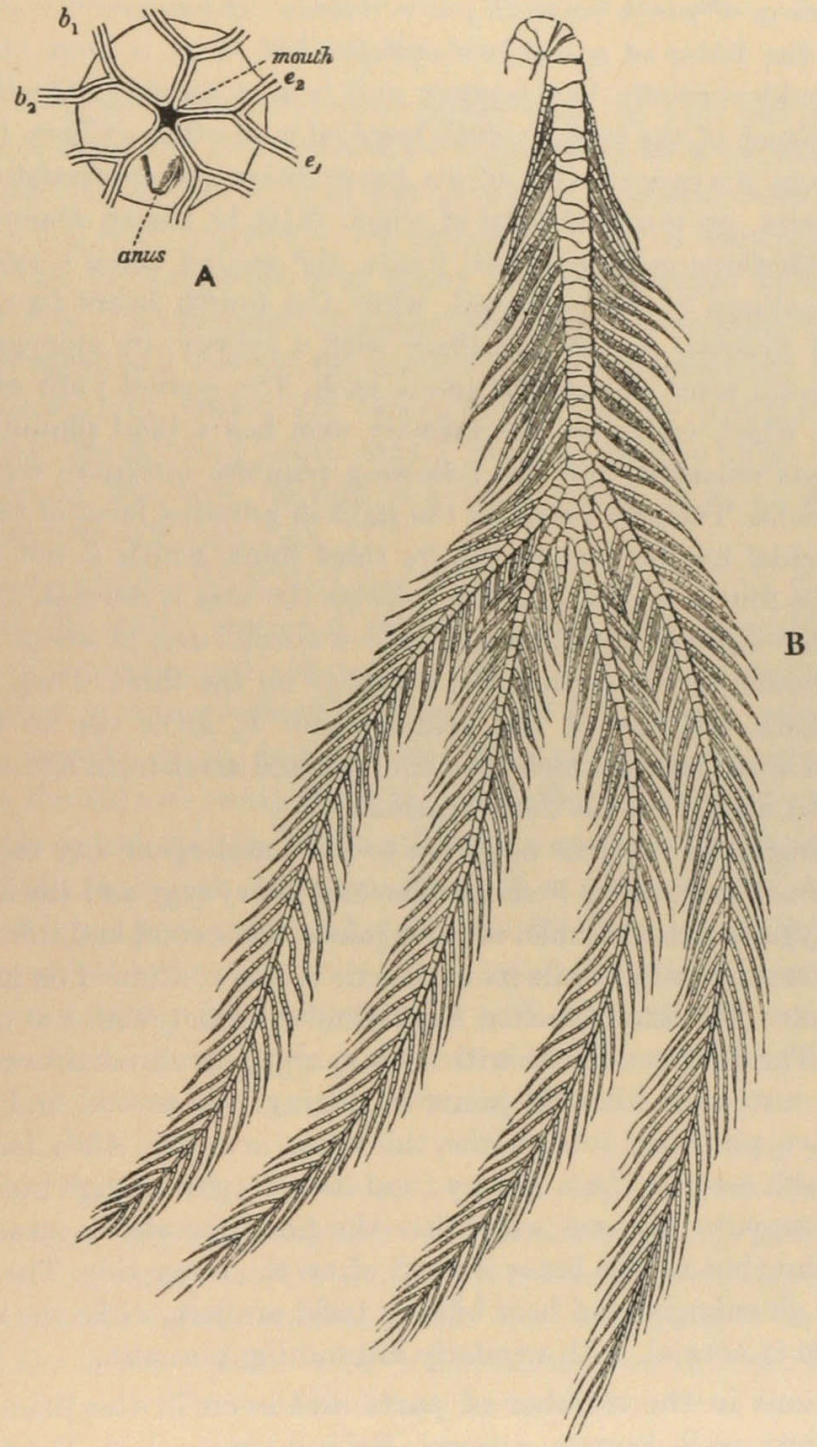


Fig. 4

A, Diagram showing the position of the abnormal arms, b_2 and e_1, to the mouth and anus. B is a semidiagrammatic enlargement of the arm, b_2.

(Drawn by Mr Edwin Wilson.)

brachial is a syzygy and its epizygal axillary. The abradial or outer facet bears an arm, of which some 75 joints remain. It has pinnules on the 2nd and 4th, the latter of which is a syzygy; but there is none on the 3rd, which would normally be a syzygy and bear a pinnule. On the larger, adradial, facet of the axillary 29th brachial is another axillary (30th br.), but without a syzygy. One of its facets bears the continuation of the primary arm, on the next joint of which (31st br.) is an abnormal trifid armlet with three enlarged basal joints, the second being a syzygy with a pinnule-stump on the epizygal, while the fourth bears two pinnules. The 32nd brachial is again axillary with a syzygy, its epizygal bearing two subequal arms of some 60 joints each. The second joint of the left-hand one which continues the primary arm has a bifid pinnule with its basal joints enlarged, and the following pinnules alternate regularly on opposite sides. The arm borne on the right or adradial facet of the axillary 32nd brachial has no pinnule till its third joint, which is not a syzygy, though the fourth is; but in other respects the arm is normal. The second facet of the axillary 30th brachial bears a normal arm of about 60 joints, with a pinnule on the second and a syzygy on the third. Thus, then, the axillary 29th brachial of the primary arm b_2 gives rise to four well-developed arms, two of which bear bifid or trifid armlets, in addition to the larger bifid armlet on the 28th brachial.

The primary arm e_1 does not seem to have undergone any regeneration and is normal to the 40th brachial. The 41st is a syzygy and the appendage of its epizygal is a short armlet of three joints, the second and third of which bear pinnules laterally, while its main axis is also continued on in the form of a pinnule. The 42nd brachial has a similar armlet, with but one lateral pinnule. The 43rd is axillary without a syzygy, its adradial branch being a normal arm with some 40 joints remaining, the second and fourth of which have pinnules, though the third has not. The 44th joint of the primary arm seems to be a syzygy; and its epizygal, though not regularly axillary, supports an arm which has the first pinnule, as usual, on the second joint, but on the inner instead of on the outer side. The next five joints are all enlarged and bear bifid or trifid armlets, while the remainder of the arm is normal, with regularly alternating pinnules.

Variations in the number of parts and even in the primary symmetries are well known among Echinoderms, but Dr Carpenter informs me that this specimen is quite unlike anything of the kind which he has previously met with.

V. *Pilchards* (Clupea pilchardus) *with the Number of Scales abnormally increased*

In the *Proceedings* of this Society for 1887 (p. 129) the late Mr F. Day described a specimen which he believed to be a hybrid between the herring (*C. harengus*) and the pilchard. The specimen was sent by Mr Dunn, of Mevagissey. Its peculiarity lay in the fact that the scales on the left side were very many more in number than those on the right side. The number of scales along the lateral line is given as 32 on the right side and 51 on the left. Mr Day adds that the ridges on the operculum, which are characteristic of the pilchard as compared with the herring, were better marked on the right side than they were on the left, though they are stated to have been very distinct on the left side also.

In the specimen described the gill-rakers were 61 in the "lower branch of the outer branchial arch" (viz. the bar consisting of the first hypobranchial and ceratobranchial), and it is mentioned that this number is intermediate between that found in a pilchard (71) and in a herring (48); but whether this intermediate number was found on the side showing the "hybrid" characters, or on the other, or on both, is not stated. These gill-rakers are also said to have been intermediate in length between those of a pilchard and those of a herring. From these points of structure Mr Day concluded that the specimen was a hybrid between the herring and the pilchard.

Before discussing the propriety of this view, I will describe two specimens showing somewhat similar characters, which were given to me by Mr Dunn during the summer of 1889. Mr Dunn told me that among the large number of pilchards which come under his notice as director of the pilchard-curing factories at Mevagissey, specimens showing this singular reduplication of the scales on one side are not uncommon. Owing, however, to the fact that the fresh pilchards are shovelled wholesale into the brine-vats, it is generally not until the fish are picked over for packing after the salting process that any individual peculiarities are noticed. This was the case with the present specimens, which were given to me as they came salted from the presses. Nevertheless, when received, they were in good condition.

The first specimen measures 8 inches to the base of the caudal fin. The head and opercula of both sides are normal. *The number of scales along the lateral line on the left side is* 32, *and the number on the right side is* 56 *or* 57. Examined closely, it can be seen that for the distance

of about an inch behind the operculum the scales are not much smaller than those of the normal pilchard, but that behind this point each scale is of about half the normal size.

The second specimen differs from the first in that the reduplication occurs on the *left* side instead of on the *right*. Furthermore, the scales are normal in size as far as the anterior end of the dorsal fin, behind which place they are of about half the normal size. The transition is much more abrupt in this specimen than in the other. The scales of this fish had been somewhat rubbed, and I was not able to satisfy myself of the accuracy of the counting, but the total number along the lateral line was approximately 48.

In the figure of Mr Day's specimen, given in *P.Z.S.* 1887, Pl. xv, no transition is indicated between normal and abnormal scales, but there is a general appearance of uniformity.

These three specimens all agree in showing repetition of the scales on one side. The distance to which this repetition extends differs in each case, but in all the condition of the scales is uniform and regular so far as it extends. In my judgment these specimens should be considered as examples of variation in number of parts. Since, however, it has been suggested that they are of hybrid origin, a few words may be permitted in criticism of this view.

No direct evidence is adduced which points to hybrid parentage. The suggestion is derived from (1) the condition of the scales, (2) the number of the gill-rakers, (3) the alleged difference in the opercula of the two sides. In view of the first point, viz. that the number of the scales on one side is intermediate between that of the pilchard and that of the herring, it seemed desirable to know whether the resemblance extended to the minute structure of the scales or was restricted to their number only. On comparing microscopically the scales of the pilchard and the herring, I find that those of the herring bear concentric lines which are almost always smooth and without serrations, while those of the pilchard are marked with lines which are waved into very characteristic crenelated serrations. On comparing the scales which are repeated, it was found that they also show these characteristic serrations and that in pattern they differ in nowise from the scales of the pilchard. This evidence appears to tell very strongly against the theory that the small scales are derived from a herring parent.

The evidence from the gill-rakers seems to be also unreliable. In a normal pilchard Mr Day found 71 on the hypo- and cerato-branchials

of the first gill-bar, and in a specimen examined by me 72 were present and in normal herrings 48. But in the two specimens showing the repeated scales there were present on the normal sides 79 and 67 respectively, and on the abnormal sides 78 in the one fish and 67 in the other. In size and shape the gill-rakers were like those of the pilchard, being smooth, and unlike those of the herring, which bear well-marked teeth.

As it is stated that the serrations characteristic of the operculum of the pilchard were very distinct on the abnormal side, it is impossible to place much stress on the circumstance that they were less distinct than those of the other side.

In addition to the considerations given above, there are several *à priori* objections to the hypothesis of the hybrid origin of these forms; as, for example, that unilateral division of parental characters is certainly not a common phenomenon, if it occurs at all, and so on. But since the evidence advanced for the theory of hybrid parentage is already open to criticism, it is perhaps unnecessary to discuss these further difficulties.

On the whole, therefore, it seems simpler to look on these abnormalities as instances of the phenomenon of Repetition of Parts, which is so common a form of variation. Though on the present occasion a discussion of the nature of these variations is to be avoided, it may be useful to mention in this connection that such repetitions are especially common among exoskeletal structures; and though, in the absence of fuller treatment, the comparison may seem somewhat crude, reference may be permitted to such cases as that of the merino sheep, etc., in which the number of hair-follicles in a given area is enormously greater than that in the common varieties. Such variations are well known among many wild and domesticated animals. The unilateral occurrence of such a variation, however, is exceptional.

The fact that these fishes were full-grown and in good condition, swimming with the shoal, should be specially remarked.

For the reasons given above it is felt to be unadvisable to consider the significance of these facts until it shall be possible to discuss the whole question of the Variation of Multiple Parts.

ON SOME SKULLS OF EGYPTIAN MUMMIED CATS

[*Proceedings of the Cambridge Philosophical Society*, VII, 1890]

SIX skulls and two restored heads of Egyptian mummy-cats were shown in illustration of the early history of the domestication of the cat. The specimens indicate that the cats embalmed by the Egyptians were of at least two kinds, and that the larger variety was of much greater size than that usually reached by either the modern domestic cat or the wild cat of Europe. These facts have been already pointed out by de Blainville and Nehring, but on comparison with a series of modern skulls it is not possible to support the attempt to refer these animals to any particular species of cat. The presumption is rather that cats of many kinds and sizes, possibly distinct, and probably including *Felis serval* and *F. caligata* (? = *F. maniculata* and *F. caffra*), were all thus embalmed; but whether these animals were all domesticated or whether some were merely collected from time to time there is no evidence to show.

Pupa-cases of the maggots which had lived in these heads were also exhibited.

ON THE NATURE OF SUPERNUMERARY APPENDAGES IN INSECTS

[*Proceedings of the Cambridge Philosophical Society*, VII, 1890]

(*Abstract*)

THE author exhibited a number of specimens in illustration of this subject.

The evidence related to about 220 recorded cases of extra legs, antennæ, palpi or wings, and particulars were given as to the mode of occurrence of these structures.

Speaking of cases in which the nature of the extra parts could be correctly determined, it was found that the following principles were generally followed:

1. Extra appendages arising from a normal appendage usually contain all parts found in the normal appendage peripherally to the point from which they arise, and never contain parts central to this point.

2. Such appendages are commonly double. The axes of the three appendages then stand in one plane, one being nearer to the normal appendage and one remote from it. In structure and position the nearer limb is the *image* of the normal limb in a mirror perpendicular to the plane in which the limbs stand, while the remoter extra appendage is the image of the nearer one in a remote mirror parallel to the first. Thus if the normal limb is a right limb, the nearer supernumerary is a left and the remoter a right, and *vice versâ*.

An extra appendage sometimes occurs which is apparently a single structure. In all instances in which the matter could be determined, it was found that the apparently single appendage in reality consisted either of two anterior halves or of two posterior halves of a *pair* of appendages conforming to the law stated. Probably therefore no extra appendage is morphologically single.

It was pointed out that these phenomena are important as an indication of the physical nature of bodily symmetry, and in their bearing upon current views of the character of germinal processes.

The author expressed his indebtedness for information, or the loan of specimens, to Messrs H. Gadeau de Kerville, Pennetier, Giard, Kraatz, L. von Heyden, Dale, Mason, Westwood, Waterhouse, N. M. Richardson, Janson, Reitter, etc., and especially to Dr Sharp for much help and advice in examining the specimens.

ON THE VARIATIONS IN FLORAL SYMMETRY OF CERTAIN PLANTS HAVING IRREGULAR COROLLAS

[*Journal of the Linnean Society* (Bot.), XXVIII, 1891]

(With Plates III and IV)

INTRODUCTION

THE following observations, which we propose to extend, are put forward as a contribution to a study of the nature of the variations by which irregular forms of corollas are, or may be, produced. As to the causes which have operated in the production of these variations, we ofler no suggestion: until a much fuller knowledge of the modes of Variation shall have been attained, discussion of the causes of Variation, or even curiosity concerning them is, in our judgment, premature.

As a problem in Evolution, the nature of the changes by which irregular corollas come into existence is especially interesting. It is, of course, well known that there is in the case of many irregular flowers strong evidence that their peculiar forms are adapted to the process of cross-fertilisation by particular insects, or otherwise. From this evidence it is naturally expected that the same is true generally for irregular corollas. This conclusion leads in turn to the deduction that the evolution of the forms of irregular corollas, as we know them, has occurred in connection with their adaptation to the purposes of cross-fertilisation, and that their perfection and persistence have consequently been achieved by the agency of Natural Selection.

As to the exact steps by which such a process may have occurred, we have no knowledge or even plausible surmise. All that we can affect to know is that each form, like other forms of living things, is a term in a series of Variations, but as to the nature and magnitude of the integral steps between successive terms there is no direct evidence. Nevertheless, to obtain such evidence is absolutely necessary before any successful attempt to get an insight into the working of Evolution can be made. If the results that we see have come about by the occurrence of a series of Variations, it is of the first importance to know what kind of series is constituted by these varying forms, and on the answer to this question all advance in the study of Evolution depends. In the absence of some knowledge of the mode in which variations occur, it is useless to guess at the relationships or past

descent of existing forms; while conjecture as to the developments which may in the future be possible to these forms is still more hopeless.

The first question, then, to be answered is this: If we had before us the whole series of individuals which have occurred in the line of descent of one given form, what *kind* of series would these individuals compose? It is too much to expect that we should discover what the series has actually been, for the evidence is gone; but we may reasonably hope to find out what are the general characteristics of such a series, for the series itself is still in progress. It is nevertheless a remarkable circumstance that a great deal of enterprise and research has of late been given up to the object of ascertaining what the actual pedigree of divers forms has been, while no one has yet succeeded in the preliminary task of determining any of the general characters of such a series. Yet if the modern conception of the manner of origin of new forms is a right one, it is a process now at this time occurring, which by common observations we may now see. Surely such observations may become the foundation of a solid and reasonable knowledge of the attributes of the method of Evolution; and when such a base shall have been established, it may perhaps be safe to attack the special problems of descent.

Supposing, then, that such a series of ancestors were before us, the matter to be determined would be the degree to which the series is continuous or discontinuous: that is to say, whether the differences between any one member and its immediate successor are so small as to be imperceptible or whether there are distinct and palpable differences between them; or whether they are sometimes small, and sometimes so great as to cause interruptions in the series and to divide it into groups of which the composing members are similar, though the successive groups are unlike each other.

The success of any attempt to comprehend the nature of the forces which are at work in the production of Variation will depend very largely on the precision with which we shall be able to answer these questions, and to determine the degree of continuity which is present in the process of Evolution. For if, on the one hand, the transition from form to form shall be found to occur by insensible and minimal changes which are so small that no integral change can ever be perceived, we should recognise an analogy with the continuous action of mechanical forces; but if it should appear that the series is a discontinuous one, and that there are in it lacunæ which are filled by no

intermediate form, the analogy would rather hold with the phenomena of chemical action, which is known to us as a discontinuous process, leading to the formation of a discontinuous series of bodies, and depending essentially on the discontinuity of the properties of the elementary bodies themselves.

It may be observed at this stage that in proportion as the process of Evolution shall be found to be discontinuous the necessity for supposing each structure to have been gradually modelled under the influence of Natural Selection is lessened, and a way is suggested by which it may be found possible to escape from one cardinal difficulty in the comprehension of Evolution by Natural Selection.

For there is one obvious consideration which makes it difficult to suppose *both* that the process of Variation has been a continuous one, and also that Natural Selection has been the chief agent in building up the mechanisms of living things. This difficulty, which is well known, may be stated thus. If the process of Variation is supposed to have been continuous, it cannot be supposed that the mechanism was at all periods of its evolution so beneficial as to be selected. For, from our knowledge of Natural History, we are led to think that while certain devices and structures may be beneficial to their possessors, yet they are so only by reason of the degree of perfection in which they exist; and that if they were materially less perfect, their utility would cease. Besides, even if there had been at some phases in their state of imperfection other functions for which they were adapted, yet still in any process of continuous evolution there must be substantially many transitional forms which are useful for no purpose, and therefore cannot be selected: in short, that the evolution of a special contrivance for adaptation is not compatible with constant and perpetual usefulness. It is clear that the degree to which this difficulty applies to any case is proportional to the complexity, perfection, and singularity of the contrivance.

In addition to the foregoing objection, a further difficulty arises when we try to figure to ourselves the kind of transitional stages by which the evolution of a complex mechanism may have been brought about. We are here met by an entire want of evidence as to the nature of such changes, and it is not easy even to conceive any hypothetical plan on which they may have occurred.

On the other hand, the objections to supposing that the process of evolution of such forms is *discontinuous* are derived, firstly, from the scarcity of observed instances of sudden and large variations, while

small variations are familiar. Secondly, there is a presentiment, which is intuitive in the minds of some, that the processes of Nature are continuous processes, and that an appearance of discontinuity is due to imperfect knowledge of these processes. With the latter difficulty we are not concerned; but it is in the hope of dispelling the former objection that the present observations are recorded.

It may be remarked that large and sudden variations have not unfrequently been observed in organs repeated in a regular series, as the petals of regular flowers, etc.; but such changes, though considerable, commonly affect all these organs equally and in such a way that the original regularity remains in the modified structure. The significance of the following examples, however, lies in the fact that they not only show the facility with which irregular systems may be converted into regular ones, but that some of them are also instances of *irregular but symmetrical* systems formed afresh, apparently as sudden variations. It will be seen that in some of these cases the resulting symmetries, though irregular, are to all appearances as perfect as those of the normal flowers.

Whether the mechanisms of the flowers thus occurring as sudden variations are useful mechanisms, and whether they are or are not adapted for cross-fertilisation by some particular insect, we are unable to say.

I. Linaria spuria

This plant, together with *L. Elatine*, is very common in both barley and wheat stubbles on heavy land round Cambridge, though almost, if not quite, absent from lighter soil. In the course of examination of a very large number of specimens of *L. Elatine*, not a single abnormal flower was found; while in the case of *L. spuria* a great proportion of plants bear abnormal flowers. The figures at our disposal do not justify an accurate statement as to the percentage of plants bearing flowers of other than normal form, but we are well within the mark in saying that these are not less than thirty per cent. of the whole number of individuals.

The area examined is bounded by the Ely road on the one side and the Madingley road on the other, extending for about four miles from Cambridge. It contains a great number of stubbles, and *L. spuria* and *L. Elatine* are very common in nearly all. The proportion of abnormal flowers was about the same in all parts of the area investigated; but in the case of a single locality lying in the parish of

Landbeach (outside the area defined above) no abnormal flower was found. All the specimens in this place were of unusual habit, having erect stems, some 10 inches in height, in addition to the usual procumbent stems. Upon these plants no abnormal flowers were found; and, speaking generally, the plants in other localities which had erect stems bore normal flowers only. Specimens of this description were not common in the district. Besides the erect position of the stem, these plants also are remarkable for the peculiar pale green colour and flannel-like texture of the leaves.

Normal Flower. (Pl. III, figs. 1 and 2).

A normal corolla of *L. spuria* is pentamerous and bilabiate, being composed of two posterior petals and three anterior ones. The two posterior petals are of a dark purple colour on the inside, while the anterior petals are primrose colour in their free portions, shading to a darker tint towards the interior of the flower; the slight inflations which occur at the points of union of the lower petals are also orange-yellow. Between the posterior petals and the anterior ones there is on either side a deep cleft which divides the two lips from each other. The sepals are five in number and are regular in size and arrangement, one being placed centrally in the upper limb of the flower. The stamens are four in number and stand opposite the lateral sepals. The two anterior stamens are a good deal longer than the posterior pair. The filaments of all the stamens bear hairs, but the hairs of the anterior pair are considerably longer than those of the posterior pair. Until dehiscence the anthers cohere. The stamen which should stand opposite the posterior sepal, if the symmetry were regular, is represented only by a filament of reduced length, and bears no anther. The pistil stands in the centre of the ring of stamens. The anterior limb of the corolla is continued into a single, hollow, curved spur. For purpose of comparison with flowers having more than one spur, it should be noted that this single spur is formed from the tissues of the median anterior petal.

Abnormal Flowers.

Peloric. (Pl. III, figs. 8–15.) As will be seen, there is great diversity of type among the abnormal flowers. The form which is perhaps more common than any other, except the normal, is of the well-known *peloric* type. In this form of flower the corolla is regular and tubular, having a general resemblance to a flower of the cowslip. The corolla has five spurs instead of one; but in many cases these spurs do not

all project from the tube, but some or all of them may be invaginated into it. This invagination may be complete or partial. In these peloric flowers the fifth stamen is always developed and bears an anther. The five stamens are of equal length, and the hairs on all of them are similar. The anthers are coherent above the stigma.

The petals of peloric flowers are generally yellow, being irregularly blotched with purple, but a few were found which were uniformly pale purple and many were seen which were entirely yellow. Peloric flowers having six sepals, six petals, and six stamens are not rare: in all of these the number 6 occurred in the stamens as well as in the corolla.

A few flowers were found having five similar yellow petals, which were not united posteriorly to form a tube, but were arranged as a single anterior lip.

An attempt was made to see whether these peloric flowers generally set seed or not, but the result was not very reliable, owing to the doubtful character of the evidence[1]. The corollas fall off as the seed-vessel enlarges, and it is then not possible to determine upon what type the flower was formed, while, on the other hand, persistence of the corolla is generally associated with atrophy of the seed-vessel. An examination of flowers which still bore the withered corolla showed that a large proportion even of normal flowers set no seed; but in several instances the seed-vessel had enlarged, and there was every appearance that the seed was sound. Out of a large number of withered peloric flowers examined, an enlarging seed-vessel containing healthy-looking seed was only found in one case; but from the ambiguity of the evidence it cannot safely be inferred that very few peloric flowers set their seed, for some of those seed-vessels which have enlarged and lost their corollas may have borne peloric flowers. On the whole the impression was produced that comparatively few peloric flowers set seed. The peloric form is well known in *Linaria vulgaris*, etc.

We shall now describe other abnormal forms in which the corolla is still irregular, though its symmetry differs from that of the normal flower. Of such abnormal flowers five forms were seen which were symmetrical, and in addition to these some of more or less asymmetrical shapes were found.

No. 1. *Flower having the corolla shaped as in the normal form, but*

[1] There is of course no question that such peloric forms set seed sometimes, but we wished to know whether they did so as often as normal flowers. Darwin, for example, raised seedlings of peloric *Antirrhinum* (*Animals and Plants*, 1885, II, p. 71); and Willdenow (*Species Plant.* III, 254) gives evidence showing that the same is almost certainly true for *Linaria vulgaris*.

possessing two spurs instead of one (Pl. III, fig. 3). Such flowers are not very common, but can generally be obtained by searching. In all those examined, the central posterior stamen (which is aborted in normal flowers) was fully developed.

Before comparing the spurs of this abnormal form with that of the normal flower, it may be remarked that the spur is of course developed from the base of a petal and not from the tissue lying between two petals. Since, then, in the normal flower the spur is an outgrowth from the base of the middle anterior petal, it is clear that if two spurs are developed and one of them is that of the median petal, the other must be formed from a lateral petal, and therefore be in origin asymmetrical. Nevertheless, in the case of flowers presenting this modification, it was often found that the tissues were so bent from their original position that the division between the two spurs came to lie in or near the median plane of symmetry of the flower. To such a degree did this occur, that it was only by tracing up the bundles in the walls of the spurs that it could be determined from which petal they were developed. In several cases, however, the original symmetry was still shown by their position.

No. 2. *Flower having one posterior (purple) petal and four anterior (yellow) petals* (Pl. III, figs. 5 and 6). This form is very common throughout our region, and occurs on a large proportion of the plants, though perhaps not quite so commonly as the peloric type. Such flowers were never seen with less than two spurs, but occasionally they have three (Pl. III, fig. 6). In all cases examined, the five stamens were all developed.

The calyx of these flowers was placed in such a position that the median vertical plane of the flower fell between two posterior sepals. Hence, though we are not able to state what the relations to the floral axis have been developmentally, yet the appearances decidedly suggest that this flower may be compared with the normal flower by imagining that *the median plane of the zygomorphy has been deflected so that it falls upon a posterior petal instead of on an anterior one.* What the circumstances may be which lead to this alteration of the plane about which the symmetry of the flower is formed, we can offer no suggestion, but we shall offer another case of a similar phenomenon in describing the variations of *Gladiolus* (*v.* p. 139).

Fig. 4 represents a flower which is in a manner intermediate between Nos. 1 and 2. For in it one of the posterior petals is partially coloured yellow, and is to some extent united to the adjacent petal

of the anterior lip. Cases of this kind, in which a petal does not stand truly with either the anterior or posterior lip, are decidedly uncommon. Such intermediate flowers always had *two* spurs and *five* stamens.

A form was frequently found (not figured) which conformed exactly with that shown in fig. 5, excepting for the fact that the deep cleft which separates the purple petal from the yellow ones was less deeply cut on the one side than on the other. These flowers had at least two spurs and five stamens. Inasmuch as the distinction between the two lips is in such cases partially absent, it may be said that this form is intermediate between No. 2 and the peloric type.

No. 3. *Flower having one posterior (purple) petal and five anterior (yellow) petals* (Pl. III, fig. 7). These flowers were not uncommon; they had *six* stamens and sometimes six sepals. None were seen with less than three spurs.

No. 4. *Flower having three posterior (purple) petals and two anterior (purplish) petals* (Pl. III, figs. 16 and 17). Of this very remarkable form only a single flower was seen. The corolla had no spur. The stamens were five in number. The filaments were not standing up in a regular arrangement, but were somewhat irregularly bent. It is not certain that this bent position of the filaments was the original one, for the anthers had already dehisced, and similar bent filaments were seen in several normal flowers after dehiscence; on the whole, however, the appearances suggested that the stamens had not been properly formed. The sepals were five in number. If this form be compared with the normal one (figs. 1 and 14), it will be seen that the symmetry is, as it were, inverted, for in this flower the posterior petals are three and the anterior petals are two, thus *inverting* the usual arrangement. In this flower, however, the three posterior petals were not closely united to form a lip, but the central one was separated by considerable clefts from the other two.

Some forms were found to which the term "monstrous" might with some propriety be applied. Chief amongst these are flowers which are built up of the parts of two flowers rolled into one. [From the analogy of other double monsters it would probably be more correct to speak of these flowers as consisting of a single flower which has partially divided into two.] This form of monstrosity is well known in many orders[1], and is not very rare in *Linaria spuria*, three such flowers having been seen by us.

[1] *Vide* Masters, *Teratology, sub voce* "Synanthy," p. 37, etc.

The peloric form of *Linaria* is perfectly well known, but the other abnormal forms which we have described do not appear to have attracted much attention.

There is, however, a good detailed account of many abnormal forms given by Chavannes[1], amongst which our form No. 2 is described and figured (Pl. VIII, fig. 1); the instance given by Chavannes is the 3-spurred variety of No. 2, and it is remarkable that his specimen of this form had only four stamens, whereas every case examined by us had five.

One form described by Chavannes (*Mon. Antirrh.* p. 66) is of especial interest in relation to some of the other varieties about to be described. This case is that of a 4-petalled *Linaria vulgaris*, in which there were two posterior petals and *two* anterior ones forming a lower lip with only a single inflation or "palate," which was destitute of grooves. This corolla had only *one* series of hairs in the interior. There were four sepals. The stamens are described thus: "*Les deux antérieures soudées en une seule plus longue; les deux autres très courtes; la cinquième stérile, mais assez développée.*" Now on comparing this with our case of *Streptocarpus* No. 4 (*v.* p. 148 and Pl. IV, fig. 1), it will be seen that a similar form occurs. In our flower the stamen standing anteriorly in the median plane was to all appearances a *single* stamen, though regarded in the way common in morphological discussions it would be presumed to be formed by the union of two, just as the posterior petal of *Veronica* is presumed by Eichler (*v.* p. 136) to be formed by the union of two petals. The question now arises whether Chavannes, in saying that the two anterior stamens were "*soudées en une seule*," meant that he believed that the single stamen had thus arisen, or was describing the actual appearance. This cannot be decided, but it is very common, and indeed usual for such modes of description to be used; and if there had been a double anther, or a double filament, or, indeed, any outward sign of duplicity, it would surely have been specified. We are inclined, therefore, to think that there was actually "*une seule*" anterior stamen as in our *Streptocarpus*; and in saying that this had resulted by the union of two, Chavannes not improbably is referring to the accepted view of the origin of such structures.

In a paper by Lafont[2], for a reference to which we are indebted to Mr Francis Darwin, a considerable number of abnormal flowers are mentioned as having been found on *L. vulgaris*. The enumeration given by Lafont includes eleven forms, but the description is without figures and is so brief as to be somewhat ambiguous in some cases.

[1] Chavannes, *Monographie des Antirrhinées*, Paris, 1833, pp. 54–74.

[2] *Ann. Sci. Nat.* (*Botanique*), sér. 2, tome XIV, p. 255.

But of these eleven forms only two clearly correspond with those found by us in *L. spuria*, viz. the peloric form and that which we have called No. 1. It is particularly to be regretted that the number of petals and stamens is not always given by Lafont. He mentions, for example, a two-lipped flower with two spurs and *six* stamens, but as the number of petals is not given it is not possible to say whether it agrees with our 6-petalled form or not. Again, he describes a two-lipped flower without spurs, but does not give the number of the stamens, which is unfortunate, since from our observations (see p. 149) there is reason for supposing that variation in number of spurs may be correlated with change in the number of stamens. It is very remarkable that among a number of varieties so large as that seen in *Linaria vulgaris* by Lafont and Chavannes, none should have corresponded with any of the several types characterised by the presence of a single posterior petal. Since this seems to be one of the most usual forms of variation in *L. spuria*, it might be expected to be frequent in an allied species. But how little importance can be attached to such *à priori* reasoning in phenomena where variation is concerned, is shown by the entire want of abnormal forms in *L. Elatine*, which is found constantly growing with and even intertwined with *L. spuria*, and which is so like it in form and colour that the two might almost pass for varieties of one species.

For a further discussion of the significance of these variations the reader is referred to the end of this paper.

II. Veronica Buxbaumii

Variations in the floral symmetry of this plant occur with extraordinary frequency. The plant is found in nearly all stubbles and waste places round Cambridge, and with two exceptions abnormal flowers were found in every locality where an examination was made. The observations were begun on the heavy land between the Histon road and the Madingley road, and in each sample of flowers from this district there were several with only *three* petals, while a small proportion had only *two*. The details of these proportions are shown in the table on p. 136. In a plot of waste garden land a few flowers were found with two posterior petals and a few with two anterior petals.

The two exceptional localities were both barley-stubbles on a subsoil of gravel, and in them no variation beyond change of size or tint was observed. These facts suggested that perhaps the heavy nature of the soil may have some connection with the presence of the

varying forms; but amongst a small number of flowers in the beds of the Botanic Garden a corolla of three petals was found. The beds were unfortunately weeded before a proper examination of these plants could be made[1].

No. of petals		2	3	4 (normal)	5 (posterior paired)	5 (anterior paired)
10 Oct.	First stubble-field	2	13	95	0	0
„	2nd „	2	16	85	0	0
„	3rd „	0	5	27	0	0
12 Oct.	4th „	1	5	6	0	0
„	5th „	0	2	118	0	0
„	6th „	0	1	30	0	0
„	7th „	0	4	329	0	0
30 Oct.	First stubble again visited	6	22	230	0	1
„	Another part of same field as foregoing	3	12	81	0	0
4 Nov.	Plot of waste garden-land	0	0	276	7	3
9 Nov.	First stubble again visited	0	6	67	0	0
10 Nov.	Stubble near Grantchester	0	7	152	0	0
	Totals	14	93	1496	7	4
	Percentages	1 %	6 %			

The flowers found in the two localities in which all were normal are not included in this table.

We now propose to describe the abnormal forms in succession:

No. 1. *Corolla with five petals, two being anterior.* According to Eichler (*Blüthendiagramme*, 1875, I, p. 210), the 4-petalled corolla of *Veronica* has been derived from the 5-petalled form of the other Scrophulariaceæ by fusion of the two posterior petals to form one. He states, further, that indications of this may be seen in the frequent occurrence of flowers with the posterior petal bilobed. For a long time no flower was found by us in which there was any suggestion of a number of petals greater than four, but at length one was found in which the *anterior* petal was paired. This specimen is shown in Pl. III, fig. 22. The posterior and lateral petals were normal. The two anterior petals were similar in colour, both having the usual pale tint of the anterior petal, but one was slightly larger than the other. In another locality three other specimens having this form were found. Two of these had a normal calyx of four sepals, but the third had five sepals, of which two were small and were placed together opposite the posterior petal. The stamens were normal in all.

[1] In this Garden large numbers of flowers having the form of Nos. 1, 2, and 3 were since found. *Vide* p. 159.

No. 2. *Corolla with five petals, two being posterior.* Of this type seven flowers were found in one locality. Instead of the single posterior petal of the normal flower, there were, in this form, two equal and distinct posterior petals. The rest of the petals, the stamens, and the pistil were normal. A flower of this type is shown in fig. 21. One of these flowers had a calyx of five sepals, the extra sepal being minute and placed between the two posterior petals.

Now if these examples had stood alone, according to current methods of reasoning they would have gone far to establish Eichler's proposition as to the phylogeny of *Veronica*; but taken in conjunction with the whole body of varying forms, there seems to be no obvious reason for considering any one form of variation to be due to reversion rather than any other. These remarks must not be interpreted as indicating opposition to Eichler's view, which seems in every way plausible; but the facts of the variation of these flowers do not establish it, since they could be used with equal force to establish the view that *Veronica* is descended from a plant with three or even two petals. The nature of the conclusions which may be deduced will be discussed after the whole body of evidence has been given.

No. 3. *Corolla with three petals.* Amongst all the abnormal forms of flowers which were found, by far the largest number are those with three petals. So common are they that they seem to form about 6 per cent. of the total. The petals in this type are of about equal size, and they are coloured and disposed as in fig. 19 (*v. infra*). Of these flowers some have only three sepals, as shown in the figure, while others have four sepals. Two 3-petalled flowers were seen with three regular sepals and a leaf-like bract borne below the calyx, upon the pedicel of the flower. All flowers with three petals in which the stamens were noted had two normal stamens, except one specimen, in which there was a third equal stamen arising from the point of union of the anterior petals.

No. 4. *Corolla with two petals.* Next to the form with three petals the 2-petalled corolla was the most frequent of the variations, occurring in about 1 per cent. of the whole number. Such corollas have the form shown in fig. 20, being composed of two petals of similar size, one being anterior and the other posterior. The calyx and other parts of these flowers were normal. Flowers of this type may perhaps be profitably compared with those of *Calceolaria*.

Asymmetrical flowers. It has been stated that no flower intermediate between any of these types was found. Two flowers, however, we found

which were asymmetrical, though they were in no sense intermediate between the other flowers. In each of these the anterior petal was large, like the lateral petal of a normal flower, and in one case the right-hand lateral petal was small like the normal anterior petal, while in the other it was the left-hand lateral petal which was thus reduced.

Plants were found bearing normal flowers together with one of the types of 5-petalled flowers, and the two types of 5-petalled flowers were not found together on any plant in one case. The 3-petalled and 2-petalled flowers were found together with each other and with the normal on the same plant.

Colour of abnormal flowers. In a normal 4-petalled flower the posterior petal is dark blue, the two lateral petals are a good deal lighter in colour, while the small anterior petal is still paler, being nearly white in some flowers.

Now in many of the flowers with an abnormal number of petals the distribution of colour followed the normal arrangement; that is to say, there was one large posterior dark petal, and the colour of the other petals became paler as the anterior middle line was approached. Sometimes the transition is so abrupt as to cause the middle strip of the anterior petal (in a 2-petalled flower) to seem nearly white; while in a 3-petalled flower, in which the division between two petals falls in the middle line, the edges of each of these is the part having the pale colour. Nevertheless, besides these, in several cases the three petals were all of a closely similar tint.

These facts show that the constitution of the flower is such that the forces by which the corolla is divided into segments are of such a kind that they *may* be disposed according to the various plans described, without necessarily involving any redistribution of the colouring. Though no conclusion can be now predicated from this fact, still it should be remembered when the time comes for attempting to apprehend the nature of the forces which thus divide the corolla into petals.

As many persons are disposed to attach importance to change of habitat and acclimatisation in promoting Variation, it should be mentioned that this plant is known to be an introduced species. Professor C. C. Babington tells us that he remembers that about the year 1827 a nurseryman of Bath showed him the plant as a new annual, and he considers it likely that it was originally imported for cultivation as a garden-plant. Soon after this time the plant had spread into a good many places, and Professor Babington recollects that he was accustomed to find it growing in a single field near

Cambridge. In the *Supplement to English Botany* (1853), 2769, the question of its origin is discussed, and it is mentioned as occurring in several places in England. Since that time it has spread everywhere, being found as far north as Aberdeen; but wherever found it is essentially a weed of cultivated land. Whether abnormal flowers are as common in other localities or at other times of the year we cannot say.

III. Gladiolus Hybrids

The next case which we propose to describe relates to changes of symmetry in the flowers of cultivated *Gladiolus*. The facts about to be presented are well known to all growers of *Gladiolus*, but, as they are of great importance in their bearing on several questions relating to variations in symmetry, it is desirable to describe them in detail.

The specimens upon which the following account is based were, firstly, a collection of Lemoine's *purpureo-auratus* hybrids in the gardens of Messrs Davidson at Ammanford, S. Wales; and, secondly, the large stock of named varieties and seedlings of *gandavensis* in the gardens of Mr Burrell, Cambridge. We desire to express our thanks to the proprietors of these gardens for the facilities they have thus kindly afforded us.

The *Gladioli* which are now cultivated in gardens are nearly all of hybrid origin, being chiefly descended from the hybrid form known as *gandavensis*. As to the origin of this form there is some doubt, and for the present the question may be deferred, a further discussion being given below (see p. 145). The *purpureo-auratus* hybrids have been obtained recently by Lemoine as a cross between *purpureo-auratus* and *gandavensis*, which, though a hybrid, seeds readily.

On examination of a few spikes of *gandavensis*, it will be soon found that the flowers are of two different kinds. In the first type (Pl. IV, fig. 6) the three segments of the outer whorl are so disposed that *one* of them (3) is anterior and median, while the other two (1 and 5) are posterior and lateral; in this type, therefore, the median plane of the symmetry bisects the anterior segment longitudinally. The segments of the inner whorl, on the contrary, are arranged in a complementary manner, so that the single *posterior* petal (6) is median while the other two (2 and 4) are anterolateral. In both cases a stamen stands in the middle plane of the symmetry; but in Type I the median stamen is *anterior*, while in Type II it is *posterior*. The symmetry of the second type seems to be that of the first inverted, for in Type II the anterior petal of the inner whorl is median, while the two others are *postero-*

lateral. The outer whorl is therefore placed so that the posterior segment is median and the other two are antero-lateral. Between these two types there are certain intermediate forms which will be described later.

The two types of flower may be found together on the same spike, or a whole spike may bear only flowers of one type. In cases in which both types occur together, it sometimes happens that one side of the spike bears flowers of one type, and the other bears flowers of the other type; in other cases, the two types occur more or less alternately on the two sides, but more usually no definite arrangement is followed. Flowers of both types, when on the same spike, are coloured alike, no matter what the colours of the spike may be; the distribution of the colouring in the two types differs in the manner to be described.

In flowers of *Gladiolus* it is usual for some of the anterior segments to be narrower than the rest, of a claw-like form, and of a colour different from that of the other segments. This difference in colour takes the form of either a striping or of a rhomboidal patch of dark or light colour upon the claw-like segments. The number of segments thus marked is partly dependent on whether the flower is of Type I or of Type II.

In flowers of Type I (which may be said at once to be the normal form of most, if not all, wild *Gladiolus*) either all three anterior segments 2, 3, and 4 are thus marked, or only 2 and 4 have this feature; but in Type II either 2 alone may be marked or 1, 2, and 3 may all be marked. But if a spike bears flowers of both types, and those of Type I have only 2 and 4 marked, the flowers of Type II on the same spike will have *only* 2 marked.

We will now describe the attitudes of the stamens in these different forms of flower. The stamens are, of course, inserted into the bases of the segments of the *outer* whorl. As in other *Iridaceæ*, they are extrorse in their position of origin; that is to say, the side of the anther upon which dehiscence afterwards takes place is turned outwards and faces the segment from which the filament arises. This position, however, is not retained in the developed flower excepting only in the case of peloric or actinomorphic flowers, which will hereafter be described. The attitude of the stamens differs according to the type to which the flower belongs. If the perianth is arranged according to the first type, having an anterior median outer petal, the stamens will be found in very nearly every case to be standing in such a way that the anthers lie parallel to each other with their faces turned

towards the anterior side of the flower. A reference to the diagram of the first type will show that, as all the stamens in this case are turned the same way, it is not possible for each of them to stand in the same relation to the segment from which it arises; and as a matter of fact it will be found that the stamen of the median anterior outer petal retains its primitive position, facing the petal, while each of the other two is rotated through 60°, so that it stands sideways to its own petal, neither facing it nor turned from it. In this way all three stamens stand facing in the same direction.

If, on the other hand, the flower be of the second type, the stamens generally assume one of three positions. In most cases the anthers do not all face the same way, but two of them, namely those of the antero-lateral segments of the outer whorl, face forwards, while the stamen of the posterior and median segment stands either in its position of origin, facing its segment, or more usually it stands sideways. In a very few flowers this stamen did also face forwards, being twisted from its original extrorse position and turned through two right angles, thus having its back to its own segment.

It is thus seen that there is very marked difference in the arrangement and symmetry of these two types of flowers, both as regards the perianth and the position of the stamens, and before describing the characters of intermediate flowers it will be well to try to realise in some degree the relation of the forms of these two types to each other.

The original ground-plan of a flower of *Gladiolus* is very simple. The flowers are arranged in two rows, one on each side of the floral axis, and at first the two rows stand back to back. Each flower consists of a perianth composed of an outer whorl of three segments and of a similar inner whorl; of three stamens arising from the base of the segments of the outer whorl; and of three carpels. The flower arises in the axil of a spathe-like bract; and opposite to this bract is another spathe-like bract, which stands between the flower and the floral axis, having its back turned towards the axis. This latter bract is recognised by Eichler[1] as consisting morphologically of two bracts united; and it has been shown by Payer[2] that it does actually so arise in development. If all parts of the flower developed equally, this flower would be regular and actinomorphic; and if each retained its original position, they would all look upwards and the two rows would stand in one vertical plane. As a matter of fact this state of things actually occurs in a good many flowers which

[1] Eichler, *Blüthendiagramme*, I, p. 161. [2] Payer, *Organogénie*, p. 659.

maintain their original regularity and position. It is of some interest to observe that these regular flowers are generally the *lowest* on the spike, that is to say, the flower which opens first[1]. Of the specimens examined a considerable proportion showed this feature; and Mr Burrell informs us that it is frequently to be seen even amongst the best named varieties, for it is not held to constitute a defect since the regular flower can be turned downwards so as to stand in series with the other flowers on the spike. In most (? all) of these regular flowers, the stamens retain their original position, each anther being turned directly outwards.

Such, then, being the original position of the flowers, by examination of the diagrams it is seen that the flower may assume either the first type or the second, according to the plane about which its irregularity is developed. The account given by Eichler relates to *G. cardinalis*, which, according to him, develops upon what we have called the second type, but, from figures of numerous species, this type seems to be exceptional.

Firstly, the original opposite position of the two rows of flowers is forsaken as the flowers open; and each flower as it opens turns horizontally towards the other row, so that the inclination of the two rows to each other is about 90°. This process is called by gardeners "making a face," and a perfect "face" constitutes a special beauty in these flowers. In addition to this horizontal rotation, each flower, instead of looking upwards, bends over so as to face outwards from the axis. This change of direction is associated with unequal growth of the different segments of the perianth, by which some of them become larger than others. The number of the segments which are thus distinguished from the rest varies greatly, and the degree to which this differentiation proceeds is also very different in the various kinds. As the result of this process of differentiation the perianth comes to be partially divided into a posterior portion, of which the segments are large, and an anterior lip, having one to three small segments. In some flowers this division is striking, but in others there is no very definite distinction between the anterior and posterior limbs of the perianth. In connection with this change of position of the flower, the radial symmetry is lost, but as the flower becomes thus irregular a marked bilateral symmetry supervenes. The fact to which we now wish to draw attention is this: that the new bilateral symmetry does not in all flowers develop about the same plane, but it

[1] In the case of several other plants, the *topmost* flower is not unfrequently peloric (*Pelargonium*, etc.).

may, on the contrary, be produced in one of two chief ways. In the first of these types the irregular perianth is symmetrical about the plane of the floral axis; and from examination of the diagram it will be seen that this plane falls in such a manner as to bisect the *posterior* segment (6) of the inner perianth and the *anterior* segment (3) of the outer whorl. This gives a flower of the form which we have called our first type, and in it the petals 2 and 4 at least are modified, the petal 3 sometimes being marked like them.

In the flower formed on Type II the symmetry is disposed about a different plane, which is not that of the floral axis, *but is the plane of that segment of the perianth which stands next to the segment which is in the plane of the floral axis.* It thus happens that the middle plane of the flower bisects the segments 5 and 2, thus falling anteriorly between two segments of the *outer* whorl. This is the condition in our second type of flower. In it either the segment 2 alone may be modified and unguiculate, or the segments 1, 2 and 3 may all be thus modified. The attitudes which the stamens assume depend upon the plane about which the symmetry is developed; the difference between them has already been described.

From examination of the figures given it will be readily seen that the flowers of both the types stand, when expanded, so that the median plane of their symmetry is vertical, and this position is gradually assumed as the flower matures. The period at which it is determined upon which plan the flower shall develop has not been ascertained, but there is little doubt that this occurs early in the formation of the bud, for examination of buds which were only just coloured showed that they were already formed upon one or other of the two types.

Flowers intermediate between the two types. It has been remarked above that, of whichever type a flower may be, it nevertheless stands in such a manner that the middle plane of its symmetry is vertical. There are, however, flowers which are formed neither upon the one type nor on the other, and these flowers stand in a position which is intermediate between those assumed by flowers of the two types respectively. Among the very large number of specimens examined at Mr Burrell's nursery, intermediate flowers were decidedly uncommon; but if an intermediate flower was found on a spike, it was usual for several other flowers on the same spike to be also of the intermediate form. A reference to the figures will at once show the characters of such intermediate flowers. The first type is characterised by the possession of *two* modified anterior segments of the inner whorl, while the second type has only one such modified segment in

the inner whorl; but in the intermediate forms, one segment is as a rule fully modified both in form and colouring, while an adjacent segment of the inner whorl, which, if the flowers were of the first type, would have been similarly modified, is only partially thus differentiated, being intermediate in size and markings between the fully modified and reduced anterior segment and the large and unmodified posterior segment. It appeared that the correlation between the reduction in size and the alteration of colour in these anterior segments is very close; for in proportion as the size of the segment is increased from the narrow form of the marked petal, so does the extent and intensity of the marking diminish. In a number of cases it was seen that the position taken by an intermediate flower is such that the reduced and marked petal (fig. 7, 2) comes to lie more nearly in the anterior middle line than it would do were the flower of the first type, but it does not lie actually *in* the middle anterior line, as it would do were the flower of the second type. This is generally but not literally true, but a few cases were seen in which the reverse was found, the partially marked petal being nearer to the middle line than the fully marked one. It was also seen that the extent to which the reduced and marked segment was displaced from the middle line was, generally speaking, inversely proportional to the degree to which the adjacent segment partook of the characters of the posterior segment; in fact the more nearly the two anterior petals were alike, the more did the flower take the position of the first type; but the greater the difference between them, the more was the position that of the second type. The position of the stamens in these intermediate flowers was somewhat various, but as a rule the anthers were turned much as in flowers of the second type. So closely does the position of the flower depend upon the degree of modification in the segments, that for a moment it seemed that perhaps the flower might be rotated into position in correspondence with some physical stimulus conveyed by the petals and varying with their size or intensity of marking. To test the existence of such a control, various portions of unopened buds were removed, but the positions assumed by the flowers on expansion differed in no perceptible way from that which they would have assumed if uninjured. Of course it must be remembered that there is no evidence as to a relation of cause and effect between the form of the flower and its position, and though for convenience we may say that flowers in which the petal 2, for example, is reduced and marked, stand so that this petal is in the median

vertical plane, it might equally be stated in the converse form, that flowers placed so that the petal 2 is in the median vertical plane have this petal marked and reduced; for all that can be seen is that the phenomena of position and marking, etc., are correlated.

The above description, as has been stated, applies to the ordinary garden varieties of *Gladiolus*, which are collectively known as *gandavensis*. As these are all of hybrid origin, the question naturally arises whether the two types of flower are both found in any wild species, and especially whether they occur in the parents of *gandavensis*. As to the first question, it may be replied at once that the type of flower here spoken of as the *first type* is the normal form of the flower in wild species. We have examined plates of a very large number of species, and have found no representation of any flower corresponding to our second type. Mr J. G. Baker, whom we have consulted on this subject, further informs us that he has never seen a wild plant having the second type of flower. Dr M. Foster also has not met with this form in the species cultivated by him. Under these circumstances it seems nearly certain that such a form occurs very rarely if at all in wild species, and that at all events it is not the normal form of flower in the parents of *gandavensis*.

It is nevertheless unfortunate that there is doubt as to the actual parentage of *gandavensis*. Herbert[1] states that it is descended from *G. natalensis* (= *psittacinus*) and *oppositiflorus*; while Van Houtte, in his Catalogue for 1844, states that it was obtained from *psittacinus* and *cardinalis*. Herbert states both here and in *Amaryllidaceæ*, p. 365, that he was unable to obtain a cross between *psittacinus* and several other species of which *cardinalis* was one. Mr Baker, to whom we are further indebted for information on this subject, inclines to the view that Herbert was mistaken.

In all figures of these flowers which we have seen they are represented as of the first type, and, as we have stated, there is no record of flowers of the second type borne by them. It is therefore very singular that Eichler[2] gives the second form of symmetry as the normal form for *Gladiolus* in general, and for *G. cardinalis* in particular. As all the other authorities consulted agree in the absence of flowers of the second type in this plant, we are disposed to think that Eichler must have taken his account from a garden-hybrid. It is not a little surprising that he should have made no mention of the

[1] *Journ. Hort. Soc.* 1847, p. 89. [2] *Blüthendiagramme*, I, p. 161.

first type of flower, which is not only the normal form of wild species, but is also on the whole the commoner even in the garden-hybrids.

The only plate in which we have found flowers of the second type represented is the coloured plate accompanying the *Gardeners' Chronicle* for Sept. 9, 1882. This illustration gives an excellent representation of two spikes, each bearing the second type of flower. For reference to this plate we are indebted to Dr Masters. No sufficient description accompanies this plate, but there is no reasonable doubt that the plants shown are garden-hybrids, which we may mention is also the opinion of Mr Baker.

It is therefore practically certain that flowers of the second type have come into existence in *gandavensis* as a variation occurring at, or since, its constitution as a hybrid, but whether such a variation ever occurs in its parents or in other wild *Gladioli* cannot be affirmed.

In conclusion, we direct attention to the following important features of the case:

(1) The same spike bears flowers of two types of symmetry.

(2) The second type of flower is of recent origin.

(3) The symmetry of the second type of flower is nevertheless generally perfect, and forms intermediate between the two types are comparatively rare.

(4) When the two forms occur on the same spike, the same colours occur in both, being distributed according to the symmetry of each, the distribution of the colours being as symmetrical in the one case as in the other.

(5) Intermediate forms, though rare, occur; the symmetry both of form and colour is in them intermediate between those found in the two types; and the position taken up by the flower is intermediate between the positions assumed by the flowers of either type, and its approximation to either position is generally proportionate to the approximation of its form to either type.

IV. Streptocarpus

We have been able to examine comparatively few flowers of this plant, and no exact record was kept of the total number of flowers seen. The observations given below were made chiefly on a batch of seedling plants of the species *Rexii*, growing in pots in a stove-house, between the months of October and December of this year. Among these plants we should say that about one in every twelve flowers was abnormal, but the proportion seems to vary greatly in

different species. These abnormal flowers are of very various types, but we are unable to say at present whether one of these types can be considered more prevalent than others; for we have had too few specimens of each to enable us to make any generalisation.

NORMAL FLOWER.

The normal flower of *Streptocarpus Rexii* is pentamerous, with a calyx of five sepals and a corolla of five petals. The corolla is bilabiate, the upper lip consisting of two petals and the lower lip of three petals (Pl. III, fig. 23). The colour of the corolla is pale greyish blue. The petals of the upper lip are of this colour without any markings upon them, but the three petals of the lower lip are streaked with bands of dark blue. There are two perfect stamens in the normal flower, situated on either side of the odd anterior petal, and two rudimentary stamens (small barren anthers without filaments) opposite the posterior and lateral sepals. In normal flowers there is a large pit about halfway down the corolla-tube, situated in the posterior middle line, and visible from the outside of the tube as a well-marked hump. A trace of an anther is generally to be found in this pit, representing an odd posterior and median fifth stamen (Pl. IV, fig. 1).

ABNORMAL FLOWERS. I. PELORIC OR ACTINOMORPHIC.

1. *Peloric flowers with* 5 *petals.* We have only seen one flower of this type on *S. Rexii*, but we have seen several on plants of *S. polyanthus* at Kew, where they seem to be of rather frequent occurrence. In the case of *S. polyanthus* the flowers we examined differed from the zygomorphic ones in standing upright instead of in a more or less horizontal position. The corolla was perfectly actinomorphic, and all five petals had assumed the character of the petals of the *lower* lip in normal flowers, *i.e.* all were streaked with bands of dark colour. There were four fertile stamens, the posterior rudimentary stamens being perfectly developed, and equal in length to the two anterior stamens. All four stamens were united by their anthers and clasped the stigma in a ring. In the flowers we examined there was no trace of a fifth stamen. The only flower of *S. Rexii* which we have seen peloric in five parts was remarkable in having *five* perfect stamens.

2. *Peloric flowers with* 4 *petals.* We have seen three or four flowers of this type, in which the calyx and corolla were reduced to a symmetry of four instead of five (Pl. IV, fig. 4). The four petals of the corolla were equal in size, and all equally marked with bands of dark

blue. The stamens were arranged in the same way as those in the pentamerous peloric flowers. In the flowers we examined there was absolutely no trace of any fifth petal.

II. Abnormal Flowers, not Peloric.

3. *Flower with cruciform, 4-petalled corolla, having* one *posterior partially unmarked petal.* Only two flowers of this type were seen (Pl. III, fig. 24). In one the calyx was in five parts, like that of the normal flower; the corolla was divided into four almost equal lobes, arranged in a cruciform manner. Three of the lobes were marked with dark blue, whilst one of them was less completely marked than the others. The four stamens were arranged in the same manner as that described above for other peloric flowers. Another flower having the same type of corolla had only two stamens as in normal flowers. The types 2 and 3 are especially interesting as showing how bilabiate, pentamerous flowers can abruptly assume a tetramerous and cruciform character, either losing their zygomorphic character altogether as in type 2, or retaining it in part as in type 3.

4. *Flowers with 4-petalled, bilabiate corolla.* Of this type we have had three specimens, two on *S. Rexii*, the other on *Streptocarpus* sp. The corolla in these flowers consisted of two upper smaller petals without markings, and two lower, larger petals with markings. In both these flowers there was one fertile stamen only, which was situated in the median, ventral line, between the two marked petals (Pl. IV, fig. 3), and two rudimentary stamens occurred laterally. Of the nature of the calyx in these flowers we have no record.

It is difficult to see how this type can have arisen unless by a discontinuous process; for by any continuous process the median anterior petal (Pl. IV, fig. 1) must have become gradually reduced, and the two stamens (S^1, S^2) on either side of it have fused into the single median one which is found in this type (Pl. IV, fig. 3). In the specimens examined there was no trace of any anterior odd petal or of any second stamen[1].

[1] An abnormal arrangement of corolla and stamens, of an exactly analogous nature, we have observed in a species of *Æschynanthus* (*longiflora*?). This flower has usually a corolla of the same pattern as that of *Streptocarpus*, and two pairs of perfect stamens, occupying a position similar to those of the two perfect and two imperfect stamens in *Streptocarpus*. In the abnormal flower the arrangement was still perfectly bilaterally symmetrical, the corolla being bilabiate with two petals in each lip, and there were three perfect stamens—one long, unpaired, median and anterior; and two shorter, paired and lateral.

5. *Flowers with 5-petalled bilaterally symmetrical corolla; 3 petals being posterior and 2 anterior.* The two flowers of this type which came under our notice had the normal number of parts to the flower arranged in an abnormal symmetry. There were only *two* larger streaked petals in the lower lip of the corolla, whilst there were *three* instead of two smaller, unstreaked petals in the upper lip. The arrangement of the stamens was only examined in one of the flowers, but in this specimen it was interesting to remark that the nature of the stamens appeared to be affected by the change in symmetry in the corolla. There were four stamens here as in normal flowers; but instead of two fertile and two infertile stamens, there was only one fertile stamen, and three infertile stamens. The fertile stamen occupied a median position, between the two anterior petals of the lower lip (Pl. IV, fig. 5). The position of the rudimentary stamens is indicated in the figure. There was no hump on the corolla-tube. If we suppose that the plane of symmetry about which the flower developed had moved round to the right through $\frac{1}{10}$ of a circle from the normal, the position of rudiments is easily comprehended.

6. *Flowers with 6-petalled, bilaterally symmetrical corolla.* Of these we have had several instances on different species of *Streptocarpus.*

(*a*) A flower from *S. Rexii*, having three petals in the upper lip instead of two, the odd median petal being somewhat smaller than the lateral ones. Stamens as in normal flower.

(*b*) Flowers from *S.* sp.?, having four petals instead of three in the lower lip, and two in the upper lip. Stamens 3 or 5 (Pl. IV, fig. 2).

7. *Flowers with 7-petalled, bilaterally symmetrical corolla.* Of such flowers we have only seen one specimen (Pl. III, fig. 25). The calyx consisted of seven sepals, and the corolla of four petals in the upper lip and three in the under lip. The stamens were normal. This flower might be described as one in which the posterior petals and postero-lateral sepals were each represented by two segments.

Asymmetrical Forms. Of these there are a great diversity, and it would not be profitable here to describe them in detail. They appear to be much more frequent on some species than others; on *S. Rexii* we have found hardly any whilst on other species they are of frequent occurrence. Forms with more than the normal number of petals are asymmetrical very much oftener than forms with a reduced number of petals.

Conclusion

In the introduction to this paper it was stated that the facts to be given bore on the question of the origin of symmetrical irregular flowers; let us now consider what that bearing is. In making the remarks which follow, it must be distinctly understood that they are put forward, not as formal theory or doctrine, but as suggestions merely, and as indications of the direction in which we must look if we hope to be hereafter entitled to formulate such definite doctrines.

It was pointed out that though modern scientific opinion has come to hold that the forms of living things have been built up by minute gradations, there is one preliminary objection to this view as applied to perfect mechanisms in general and to irregular corollas in particular, namely, that there is no evidence as to the mode by which the process of building has been, or even might have been, carried out; for indeed we can hardly suggest or even conceive a way by which, in a concrete case, a perfect mechanism can have been compiled out of minimal changes. The objection holds, that these forms are in a sense perfect, and we cannot conceive them otherwise. On the other hand, there is the difficulty that it cannot be maintained that the progress of Evolution is from one perfect form to another perfect form, until evidence shall have been found showing that this process does occur as an actual phenomenon. The facts now given, though few, are a contribution to such evidence and, in our judgment, are a sample of the kind of fact which is required to enable us to deal with the problems of Descent.

From each of the plants studied, truths of specific application may be learned; but there is one fact which they all bring out together, and that fact, which is of fundamental importance to the right comprehension of the modes of Variation, is this: (1) *Variations which occur in such a manner as to produce a symmetrical result may be great variations and may be perfect*; and conversely that (2) *Variations which are large do often produce a symmetrical result*; and (3) *that the perfection or completeness in which a variation in symmetry occurs is not, or at least need not be, proportional to the frequency of the occurrence of the variation.*

In other words, there is evidence that perfect forms may occur as sudden variations. Hence, in any given case, of the actual history of which nothing is known, it is unnecessary to invent a hypothetical method by which its perfection may have been achieved by the

compounding of minimal changes; and to propose such an hypothesis is to gratuitously invoke difficulty. The principle which we have put third, plain as it is upon the facts of Variation, is most imperfectly recognised, and indeed, in the loose consideration so often given to this subject, the very contrary is frequently assumed.

We are therefore led to recognise that the forces which control the forms of these flowers are such, that they may vary greatly, and may, as it were, remake the flower; but the flower thus remade may again seem to be a perfect thing in the sense that the normal flower is perfect, for at least that semblance of perfection which is found in the one is likewise found in the other. What those forces are which thus control the form of the flower, and how, or why, they thus combine to form symmetrical shapes we cannot tell; but the fact that they can do so, and that this is one of their attributes, may one day be found to be the clue that shall discover to us the nature of those forces.

Certain reservations must be borne in mind.

At the outset of the study of Variation, it is at once found that argument from analogy from one organ to another, or from the case of one organism to that of another, is as yet inadmissible; for the variation of special organs or of specific forms is frequently governed by principles which, so far as we can see, are likewise specific. We are therefore conscious that it is by no means legitimate to affirm principles like the foregoing as *general* principles of symmetrical variation; but that these principles are obeyed in the special cases now under consideration is sufficiently clear. Still the fact that such principles are found operating in certain cases should at least suggest the possibility that the same principles may have been followed in other cases; and especially when a form (*e.g. Veronica*) is found whose symmetry is related to that of its presumptive allies in a way similar to that in which the varieties now described are related to their respective normals, it may not be unreasonable to suspect that variations of this discontinuous character have occurred.

There is, however, another reservation which is of more importance. In all the cases now given of a new zygomorphic symmetry arising as a sudden variation, the new form has resulted by variation from another zygomorphy already existing, and not from a regular or actinomorphic flower. From such evidence, therefore, it would be wrong to draw conclusions as to the mode of origin of a zygomorphic flower from an actinomorphic one. Therefore, though the facts

warrant the statement that a new form of zygomorphic corolla may occur as a sudden variation, this may as yet be affirmed only in the case of an irregular symmetry derived from another symmetry itself irregular. For example, the facts lead us to suspect that such an irregular, 4-petalled corolla as that of *Veronica* may have occurred as a sudden variation from the form of some 5-petalled Scrophulariaceous ancestor; but we are as far as ever from knowing how that irregular corolla of the ancestor was derived from a regular or actinomorphic form. At all events the facts now given have no direct bearing on this part of the problem.

We do not now propose to attempt a discussion of the facts in their specific bearing, for the material is not such as to entitle us to do so, still less can we aim at an analysis of the various forms of symmetry presented.

It may, however, be pointed out that the examples taken show two methods by which a change of symmetry may be effected, and it is clear that these two processes are essentially distinct phenomena. For while, in the majority of instances given, the change of symmetry comes about by an alteration in the number of the parts, the case of the variation described in *Gladiolus gandavensis* and that of *Linaria spuria* No. 2 are alike in that they exhibit a change of symmetry attained not by an alteration in the number of parts, but by the selection of a different morphological plane about which the symmetry is developed. For inspection shows that in each of these cases the normal plane of symmetry of the flower has been forsaken and a new one substituted, so that the plane about which the symmetry of the flower is arranged falls through one of the segments adjacent to that through which it normally falls, and the parts of the flower are rearranged accordingly, but the number of the parts remains unchanged. Change of number of parts may also be associated with this alteration in the plane of symmetry, as is seen in the flower of *Linaria* No. 3 (Pl. III, fig. 7). In other cases given, the change of symmetry is accomplished by a change in the number of parts. In *Veronica* for instance, though a zygomorphic arrangement of 4 petals is normal, perfectly zygomorphic arrangements of 3 and 2 petals were shown to occur, in addition to two types of symmetrical flowers each with 5 petals.

At this stage it may be well to point out that in the cases given no assistance in the interpretations of their completeness is to be derived from the suggestion that these variations are instances of reversion to an ancestral type.

To some persons it seems more easy to conceive the occurrence of

a perfect variation back to an ancestral form than to a form which has not occurred in the lineal descent, and Reversion is not unfrequently invoked to account for large or complete variations, though what help is derived from such an hypothesis is not clear. It is likely that the study of Variation will hereafter lead to and necessitate a revision of the whole question of the nature of Reversion, but this is no part of our purpose at present. It must suffice to show that the hypothesis is inadmissible in most, if not all, of the present cases. The reasons for this are two: (1) In the case of *Linaria*, *Veronica*, and *Streptocarpus* several distinct and symmetrical forms have been shown to occur as variations. It is practically inconceivable that each of them is an ancestral form, and indeed such a suggestion is almost meaningless. Since, for example, the form *Veronica* No. 2 closely approaches the usual form of other *Scrophulariaceæ*, it might reasonably be thought to be a reversion, but the forms Nos. 1, 3, and 4 cannot also be reversions. (2) The instances in which the strongest case for the hypothesis of Reversion could be made out are probably those of the peloric *Linaria* and the peloric *Streptocarpus*. For good reasons we suppose an irregular flower to be descended from a regular one; these flowers are regular, may not they be ancestral? This is a fair suggestion, but it introduces certain difficulties. For the peloric flower, in each case, is achieved not by the production of 5 *indifferent* petals, but by the production of 5 petals each *like the normal anterior median petal*, each having in the one case a nectary, and in the other the definite striping. Now the possession of a long spur-like nectary is a character of many irregular corollas, and is commonly supposed to be one of the essential parts of the mechanism of cross-fertilisation, and on the ordinary view would be held to have been developed in connection with the irregularity of the corolla to attract the insects to the right place, for the presence of spur-like nectaries in actinomorphic flowers, as *Aquilegia*, is exceptional. Similarly the striping on the anterior petals of *Streptocarpus* may reasonably be looked on as part of the mechanism for attracting and guiding insects. Though, therefore, we do not wish to dogmatise in such a case, it must be clear that it is not possible to hold *both*—(*a*) that the spur-like nectary or the striping of the petals are part of the mechanism for cross-fertilisation which is the presumed purpose of an irregular flower, and also (*b*) that these actinomorphic or peloric flowers are reversions to an ancestral type. For our own part we prefer to look on them as cases in which each petal has taken on the form of the anterior median

petal of the normal flower, just as stamens may take on the form of petals, etc.; for we are not disposed to believe that the ancestor of *Linaria*, which had a regular and actinomorphic corolla, was possessed of five spurs. This has been fully discussed by Masters[1], who describes this phenomenon as "Irregular Peloria."

In some of the cases given, as in the *Veronica* and the flower of *Linaria* No. 4, no flowers were found having a symmetry intermediate between that of the variety and the normal; but in other cases, as between the two types of *Gladiolus* and between *Linaria* No. 2 and the normal, a considerable number of intermediate forms were seen. But since the descent is not from flower to flower, but from plant to plant, and since the same plant may bear normal flowers and flowers having the perfect symmetry of the variety as well as intermediate flowers, the presence of these occasional intermediate flowers in no wise enables us to avoid the conclusion that in the case of an individual flower as opposed to an individual plant the change is a sudden one. Still less does the presence of some amorphous flowers, such as occur in *Linaria* or *Streptocarpus*, at all modify the fact that the flowers are capable of assuming, and often do assume, the form of the variety in its perfection. Since, besides, these amorphous flowers are not intermediate between the normal and the perfect variety, it is not necessary for us to take cognisance of them in considering the relative numerical proportions of the intermediate form as compared with the perfect variety or the perfect normal.

The next consideration which suggests itself as a deduction from facts like these is of far-reaching consequence, and touches the nature and soundness of the received principles by which morphological facts are interpreted. It is manifestly impossible to give any adequate discussion of such a subject within the limits of this paper; and it is only on a much wider survey of the facts of Variation that the real force and legitimacy of this deduction can appear. Since, however, the facts now presented lead naturally to this question, it may be right to give a slight forecast of the line of thought which they suggest.

The whole significance, then, of facts of comparative structure, and especially of the facts of development, as applied to the study of Evolution, lies in the belief that the genetic relations of species and genera *can* be determined from this comparative study of their forms and modes of development. In other words, it is supposed that the changes by which species have been evolved from each other are of

[1] *Vegetable Teratology*, p. 228, etc.

such a nature that, speaking generally, it is from time to time possible to perceive their relationships by study of their forms; and especially it is anticipated that these changes are of such a kind as to leave more or less recognisable traces of their occurrence. In proportion as it shall be found that variations occur *without* leaving such traces of the previous form of the species, to that degree will comparative study of form and development be powerless to solve the problem of Descent. Now, though it is a question which needs more investigation, it is at all events apparently true that the changes which leave traces are continuous changes, while discontinuous changes leave little or no trace; so that the principle may probably be stated thus, that in proportion as Variation is not a continuous process will comparative morphology cease to be an effectual guide to the history of Descent.

The facts of the changes seen in our flowers show, as has been said, that when a change of symmetry is concerned, Variation is constantly discontinuous, leaving no visible trace. It is therefore in the case of forms of differing symmetries that we must expect the evidence of comparative morphology to be absent or inadmissible. Yet it is precisely at this very point of alteration in symmetry that we want help as to the history of Descent. It is easy to conceive the steps between forms differing in the degree of expression of some character, such as size or intensity of colour, but in trying to pass from a form with one kind of symmetry to a form with another we often cannot even conceive the transitional steps. There are some cases in which such steps can be conceived and are assumed to have occurred. In *Veronica*, for example, when compared with other *Scrophulariaceæ*, it is supposed that the flower of the former has been derived from the latter by "fusion" of the two posterior petals, by loss of the posterior median sepal, by abortion of stamens, and the like. The study of Variation shows how vain and inadequate this treatment is. In the *Veronica* with three petals is it supposed that there has been, firstly, division of the anterior petal into two parts, each of which has united with the lateral petals? What is the evidence of this? Let it be remembered that in suggesting that the posterior petal of *Veronica* has been formed by union of the two posterior petals of its Scrophulariaceous ancestor, it is certainly suggested that there has been a series of actual forms in which this union was, step by step, effected, and that the occurrence of occasional flowers with two posterior petals like our No. 2 is a proof of this. But what, then, does the flower No. 1 prove; for in it there are two *anterior* petals? Where are the

transitional forms between the 2-petalled and 3-petalled flowers and the normal? These forms are now arising at this moment on the very plants which bear the normal flowers, and intermediate forms, if indeed there are any, are so rare that we have found none. If there are no transitional forms in the one case, why need there have been transitional stages in the other[1]?

Take, again, the case of *Streptocarpus* No. 4: comparing it with the normal flower, it is seen that the median anterior petal is not "becoming aborted," but is *gone* (Pl. IV, figs. 1 and 3). Now if this petal had gradually disappeared, the two stamens which in the normal flower stand on either side of it would have come nearer and nearer together until, on the total disappearance of the median anterior petal, the two stamens would stand together. But in this specimen there were not *two* stamens but *one* stamen, which tells the plain story that no such process of gradual atrophy of the anterior petal has occurred at all. On the contrary, the forces which combine to make the normal flower were driven instead to make the flower No. 4, and succeeded in making it, a symmetrical and perfect thing—perfect, that is to say, in the sense that the normal flower is perfect.

How, then, if the seed of this flower had been saved and a race of *Streptocarpus* having the symmetry of No. 4 had arisen? Such a thing may be possible enough. By what means would the morphologist of the future have traced the descent of this flower by comparison, and so forth? Of course we recognise that had it been possible for us to have observed the development of this flower, some indication of a change of plan might perhaps have been found; but if all trace of such a great and essential change as this is at the moment of its occurrence thrust far back into development, the prospect of finding traces now of any large proportion of the changes which happened long ago is not hopeful. We are therefore disposed to think that the first teaching of the facts of Variation is this: that *comparison* of forms is not likely to be a good guide to the history of

[1] The following piece of evidence may not be without interest in this connection. It is stated with regard to *Scrophularia arguta* that towards the end of summer the lowest branches springing from the stem bend downwards and penetrate the soil; the branches immediately above the lowest ones also bend downwards, but do not always enter the earth. These branches bear fertile flowers; those which are below the soil are completely destitute of petals; those which are on the surface have a four-lobed corolla whose divisions are nearly equal, like those of *Veronica*. The above account is taken from Masters, *Vegetable Teratology*, p. 334, and the original observation is recorded by Durieu de Maisonneuve in *Bull. Soc. Bot. France*, III, 1856, p. 569, but unfortunately contains no information beyond that given here.

those forms; and that there is no evidence that degrees of apparent relationship of form are an indication of degrees of actual relationship by descent; and that nothing short of an actual knowledge of the processes of Variation and a discernment of the changes which are possible to living things from those which are impossible to them, can be of any use in the solution of the problem of Descent. Until such knowledge shall have been reached, any hypothesis of the "atrophy" of parts, of the "fusion" of parts, and generally the attempt to reconstruct what is unknown, must, of necessity, be unfounded and misleading, and had better not be undertaken.

The fact that there are certain Variations which are, as it were, integral, and which, if they occur at all, occur in their complete form always, or nearly always, is of course perfectly well known. Darwin[1] gives several cases of this as illustrations of the phenomenon that certain characters cannot blend. In particular he instances the case of peloric *Antirrhinum*, which is closely akin to *Linaria*. He states that of 137 plants raised as the second generation of a cross between normal and peloric *Antirrhinum*, only two were in an intermediate condition, while the others were all either normal or peloric. Our object now is to show that this principle is widely true of variations which are of the nature of specific changes, and to point out that it may help us to measure the size of the integral steps of Variation.

An objector may say that there is no evidence that the Variations we have described are such as lead to the formation of new species and new forms. That is perfectly true; but nevertheless it is clear that they *may* be of this nature, and that new forms *might* thus originate; and while, on the other hand, there is no evidence of the occurrence of Variations other than these, by which new forms of symmetry may be produced, this class of Variation is entitled to be very carefully considered. For our own part, we think, further, that evidence can be adduced to show that this class of Variation does lead to the formation of distinct forms; but this is a much wider subject and must needs be postponed for the present.

There is, however, another class of Variation which is known to occur, and space will not be wasted if we point out very briefly the relation of this other kind of Variation to that described by us. By the elaborate researches of Galton[2], it has been shown that the

[1] *Anim. and Pl.* 1885, II, p. 71; see also Mélicocq, in *Bull. Soc. Bot. France*, 1859, VI, p. 716.

[2] F. Galton, *Natural Inheritance*, etc.

frequency of the occurrence of certain Variations obeys the Law of Error; that is to say, that, speaking generally, the greater the departure from the normal form, the rarer will be the Variation. Galton has shown that this is true of several Variations in size, etc., of Man; and Weldon[1] has further established the same for Variations in proportional measurements of the shrimp (*Crangon vulgaris*), etc. Though these are the only Variations which have been properly investigated by a statistical method, it may be seen by inspection that the resulting proposition cannot be true of the Variations which we have been considering. For in these cases of symmetrical Variations, as we have shown, the Variation is frequently complete and seldom incomplete, and the perfection of the Variation is out of all proportion to the frequency of its occurrence. If we suppose in the case of *Linaria spuria* that the flowers having the normal form or the form No. 2, or some intermediate form, could be arranged in a series, it would then be found that there were a great number of normals, a few intermediates, and a considerable number of flowers with the form No. 2. The form No. 2 is thus, as it were, another normal. It is no doubt true that flowers having substantially the form No. 2 vary also among themselves; and it is possible enough that the comparative frequency of these Variations obeys the Law of Error, taking the form No. 2 as the mean form. It seems, in fact, in cases where changes of symmetry are concerned, that the intermediate forms are, as it were, points of unstable equilibrium, and that the body therefore assumes these forms rarely, as in some instances, or never, as in others. A simple illustration, though somewhat loose, may make this more clear.

The distribution of forms with regard to the normal symmetry, on the one hand, and the symmetry of the variety, on the other, may be perhaps compared with the spread of agricultural settlers into a country divided by a mountain-range. The mass of the people will settle in the nearest plain. Some will perhaps settle on the hillside, but these will be found fewer and fewer as the range is ascended; but those who get over the top of the range will mostly go down into the plain beyond. Those in the hither plain are many and are the normal; those in the valley beyond are the variety, and the few on the hillsides are the intermediates.

We wish, then, to insist upon the fact that there are at least two classes of Variation; and it is suggested that this is a fact of great

[1] W. F. R. Weldon, *Proc. Roy. Soc.* XLVII, 1890, p. 445.

importance. It may be remarked that if, as may be alleged, there is little evidence that species may arise by what may be called discontinuous Variation—a Variation in kind—there is still less evidence that new forms can arise by those Variations in degree which at any given moment are capable of being arranged in a curve of Error; and no one as yet has ever indicated the way by which such Variations could lead to the constitution of new forms, at all events under the sole guidance of Natural Selection. Whatever may be hereafter determined as to the scope of either of these classes of Variations in the constitution of Species, it is of the first consequence to recognise that these two classes of Variation exist; and the problem of the history of any given form or structure will never be solved until it shall have been first determined whether it is the result of the one class of Variation or of the other, and whether the changes which produced it were continuous or discontinuous.

NOTE. The observations above recorded were made a year ago, and as since that time the case of *Veronica* has been much more fully investigated, a brief abstract of these observations may here be added.

In *Veronica Buxbaumii* 3-petalled flowers are common on all soils and in many gardens round Cambridge, though entirely absent in a few localities, according to our experience. This type most frequently has 4 sepals, but 3-sepalled specimens are not rare. Flowers with 5 petals having the form either of No. 1 or No. 2 are also fairly common, especially in gardens. Speaking generally, there are in garden soil not less than 1 per cent. of each of these forms in many localities. Several forms of *asymmetrical* corollas have been seen, but they are rare and are generally associated with petalody of stamens. The latter phenomenon is rare, and is seen especially in the case of certain dwarfed corollas which are sometimes found. These curious flowers are very interesting, but cannot be satisfactorily described in so short a note.

In the Cambridge Botanic Garden the two kinds of 5-petalled flowers are very common on *V. austriaca*, *V. rupestris*, and *V. pectinata*. In the patch of the last-named form at the Gardens abnormal flowers are as frequent as normal ones, and about a quarter have petalody of one or both stamens or other complex malformations. "Synanthy" is also common in this form.

On *V. Chamædrys* two flowers of the 3-petalled type were seen this year on separate plants. The 5-petalled form of flower with two posterior petals also was found sparely. Abnormal flowers in this species appear to be decidedly rare.

Explanation of the Plates

PLATE III

Figs. 1–17. *Linaria spuria*; normal and abnormal flowers.
(For simplicity the hairs on the sepals are mostly omitted.)

Fig. 1. Normal flower, seen from in front.
Fig. 2. Normal flower, seen from the side.
Fig. 3. Flower having corolla normally divided, but with two spurs instead of one (and five complete stamens).
Fig. 4. Flower intermediate between that shown in Fig. 3 and that shown in Fig. 5 (rare).
Fig. 5. Abnormal flower, No. 2 (in text).
Fig. 6. Abnormal flower, similar to that shown in Fig. 5, but having three spurs instead of two.
Fig. 7. Abnormal flower, having one posterior petal and five anterior ones—six in all.

In Figs. 5, 6, and 7 the anterior sepal is not shown.

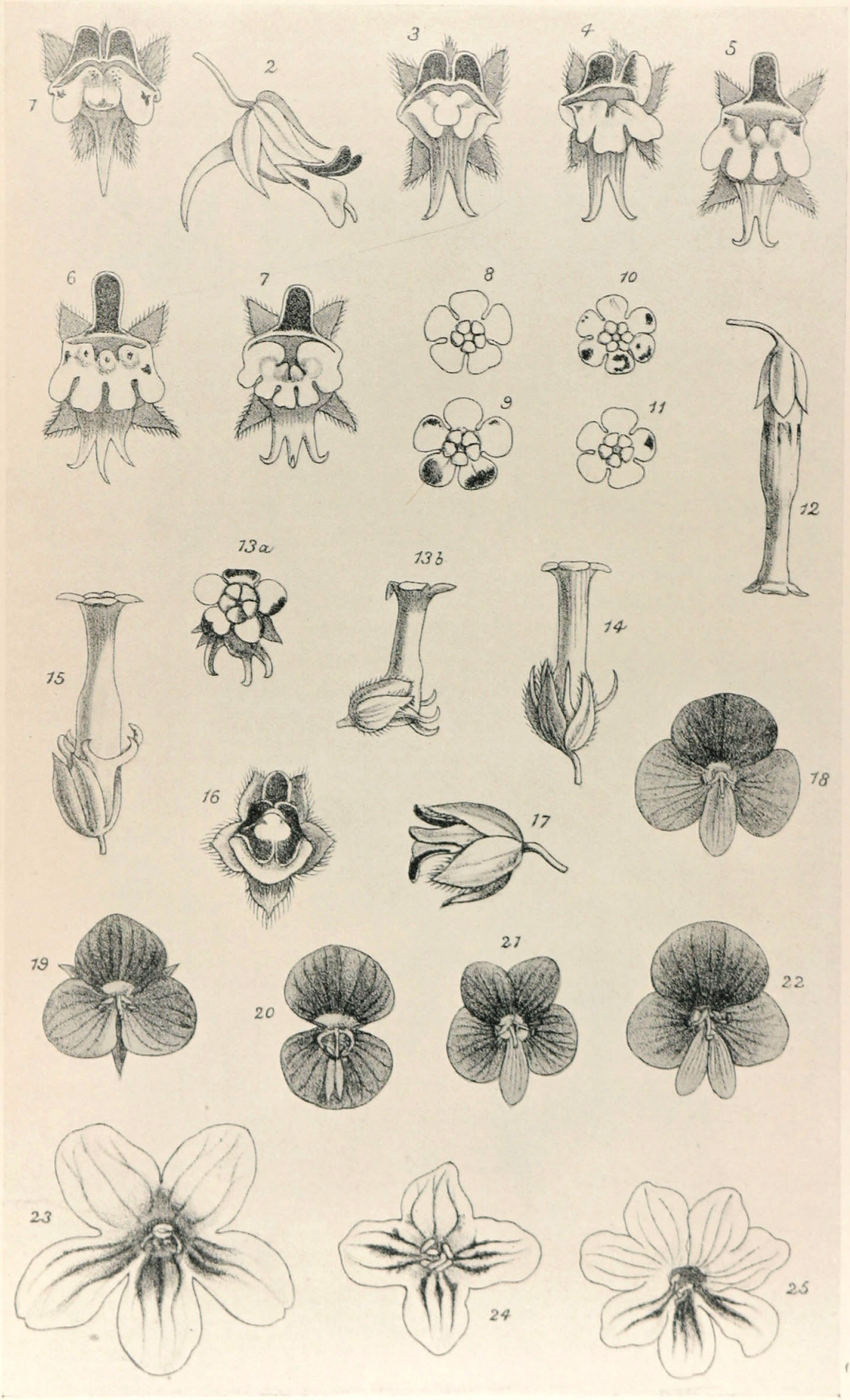
Figs. 8, 9, 10, 11. Various forms of actinomorphic (peloric) corollas, seen from above. That shown in Fig. 10 has six petals.
Fig. 12. Actinomorphic flower with all the spurs invaginated into the tube at the points.
Fig. 13 *a*. Corolla which is actinomorphic as regards the size of the petals and the division of the tube, but having the posterior petal folded back and the corolla bent upwards, as shown in the figure.
Fig. 13 *b*. The same flower, from the side.
Fig. 14. Actinomorphic (peloric) flower having five spurs, all evaginated.
Fig. 15. Actinomorphic flower having six petals and six spurs, all evaginated.
Fig. 16. The abnormal flower described in the text as No. 4. Only a single flower of this pattern found. It has three posterior (purple) petals and two anterior (purplish) petals. Seen from in front.

Figs. 18–22. *Veronica Buxbaumii*, normal and abnormal flowers.

Fig. 18. Normal flower.
Fig. 19. Three-petalled flower (about 6 per cent., see p. 137).
Fig. 20. Two-petalled flower (about 1 per cent.).
Fig. 21. Five-petalled flower, two petals being posterior.
Fig. 22. Five-petalled flower, two petals being anterior.

Figs. 23–25. Figures of *Streptocarpus Rexii*, normal and abnormal.

Fig. 23. Normal flower.
Fig. 24. This flower had four petals, three being fully marked as normal anterior petals are, the posterior petal being less marked. Four perfect stamens and *five* sepals, one being posterior and median. This flower was therefore intermediate between a normal flower and the peloric flower with four parts. Cf. Pl. IV, fig. 4.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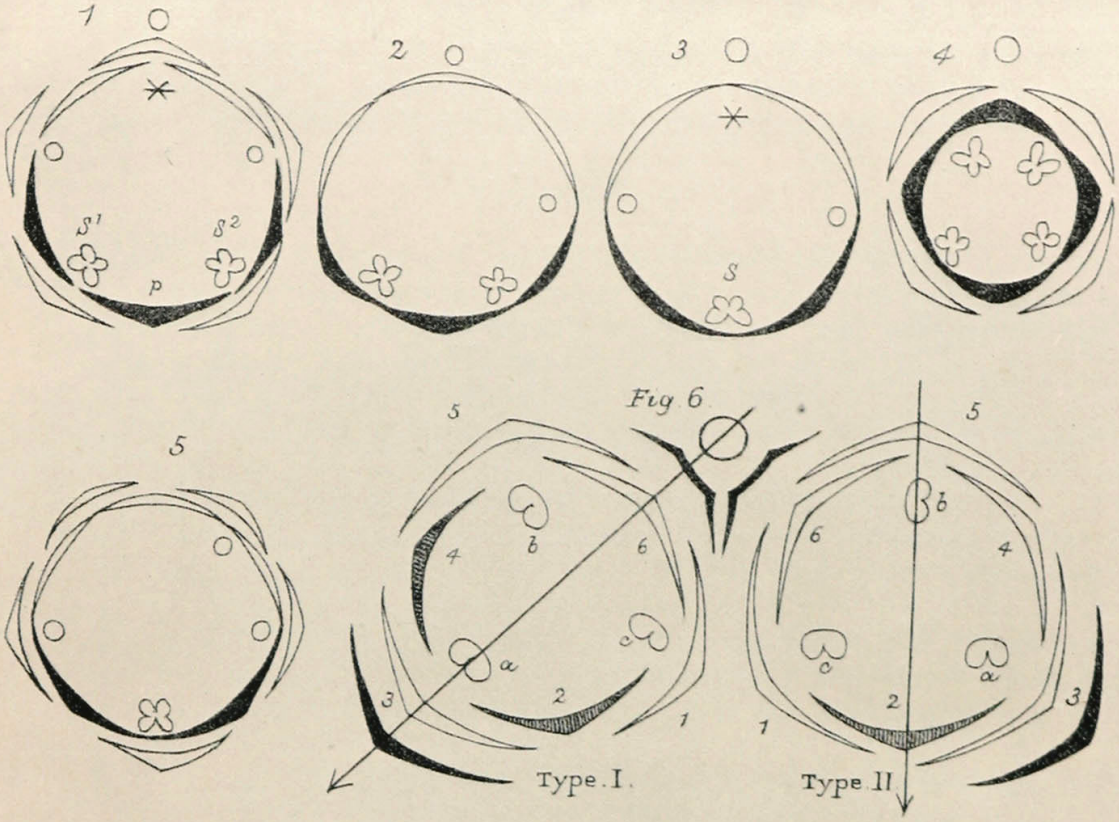
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Fig. 25. Flower having three anterior marked petals and four posterior unmarked petals. This flower has seven sepals in correspondence with the seven petals, but the stamens were as in the normal flower, viz. two perfect and two aborted.

PLATE IV

Figs. 1–5. Diagrams showing the disposition of the corolla and stamens in *Streptocarpus Rexii*. The ovaries are not shown, as their relation in the abnormal cases was not satisfactorily made out. In each case the petals which were marked like the normal anterior petals are blackened.

Fig. 1. Normal flower: two posterior and three anterior petals.

Fig. 2. Flower having three posterior and three anterior petals. Corolla and stamens only.

Fig. 3. Flower having two posterior and *two* anterior marked petals. Observe that in this flower a single stamen stands anteriorly, *in the plane about which the flower is symmetrical*; while in a four-petalled flower, like Fig. 24, in which all the petals are marked, there are four complete stamens.

Fig. 4. Flower having three posterior petals and *two* anterior petals. Only one stamen is developed. The axis is not shown in this case, as its relation was not satisfactorily made out, but the attitude of the flower was that indicated in the diagram.

Fig. 5. Actinomorphic (peloric) flower with four petals, sepals, and stamens. *All* the petals were marked as anterior petals of the normal flower.

Fig. 6. Conventional representation of the parts of the flower in the two types of *Gladiolus gandavensis*, showing the planes about which their zygomorphy develops in each case respectively. N.B. The anthers are shown in the positions which they commonly assume in the expanded flowers of each type. In flowers of Type II the anther *b* not infrequently retains its position of origin, *facing* the segment 5; rarely it turns completely round so as to face the segment 2. The "unguiculate" are shaded darkly.

Fig. 7. *Gladiolus gandavensis*, Type I, from same spike as Fig. 4 (from a photograph).

Fig. 8. *Gladiolus gandavensis*, Type II, from the same spike as Fig. 3 (from a photograph).

Both are from the same side of the spike.

[Plates III and IV are printed from process blocks made from the lithographs of the original paper. ED.]

ON VARIATION IN THE COLOUR OF COCOONS OF *ERIOGASTER LANESTRIS* AND *SATURNIA CARPINI*

[*Trans. Ent. Soc. Lond.*, 1892]

It is well known that the cocoons of certain moths are sometimes dark brown and sometimes of various lighter shades of colour, being occasionally quite white. This variation is well known in the case of the small egger (*Eriogaster lanestris*), and the emperor moth (*Saturnia carpini*).

It has been suggested by Poulton[1] and others that these colours are of value as a means of concealment from enemies, and it has been stated by them that the variation in colour of these cocoons accords with that of the substances to which the cocoons are attached. In the place referred to, Poulton says:

I found that caterpillars of this species (*S. carpini*) spun very dark brown cocoons in a black calico bag, while white cocoons were spun in white surroundings in a strong light. In this case it seems almost impossible for the surrounding colours to influence directly the colour of the cocoon. It is necessary to assume the existence of a complex nervous circle as a medium through which the stimulus of colour can make itself felt.... The Rev. W. J. H. Newman showed that the cocoons of *E. lanestris* are creamy white when spun on white paper, dark brown when constructed among leaves.... The fact that light reflected from green leaves is here the stimulus for the production of a dark colour is readily intelligible when we remember that the moth does not emerge till the following February at the earliest, while the insect often remains in the pupal state for one or two years longer. The leaves in contact with the cocoon soon die and turn brown, and after this change the dark colour is highly protective. It is also of especial importance for the cocoon to be well concealed during the winter months, when insect-eating animals are pressed for food, and are obliged to search for it with extreme care.

An experiment with *Halias prasinana* is then described, in which a larva which had begun to spin a *brown* cocoon on an oak-leaf was transferred to a white box, where it subsequently spun a *white* cocoon.

If it were really established that there is an intimate relation of this kind between the colour of the cocoon and that of the substances to which it is attached, the fact would be very surprising, and perhaps

[1] E. B. Poulton, *Colours of Animals*, 1890, pp. 142–146.

unparalleled. We have here to deal with a case not of a graduated resemblance between the general tint of the skin of an animal and that of the ground on which it lies, such as is found in many forms which are provided with contractile or movable chromatophores (the sole, *Sepia*, etc.), but of a resemblance between the colour of external objects and that of a secreted substance poured out upon them. The existence of such a phenomenon, if proved, would introduce new possibilities into physiology.

It is, of course, believed that this power of adapting the colour of the cocoon is a protection from enemies, and it is suggested that as such it may have arisen and been perpetuated by Natural Selection. To this view there is an objection which may be widely applied in like cases, but which in this one has particular force. The belief that the resemblance between the cocoon and adjacent objects protects the insect is based on expectation and not on evidence. If we ask from *what* enemies the insect is thus protected, we are told from insectivorous enemies; and here the matter must rest. There is as yet no direct evidence that a definite bird or mammal, for instance, has ever been seen to open a cocoon of *S. carpini* or *E. lanestris*; still less that any such animal habitually searches for these cocoons. In the case of *S. carpini*, at least, it may be plausibly argued that, so far as *à priori* impression goes, it is unlikely that these cocoons are sought by birds, for the wall of the cocoon is so tough that it must be difficult for most birds to pierce it. No doubt rats and mice could gnaw through them, but it is likely that these animals, which are for the most part nocturnal, depend for their supply of food at least as much on the sense of smell as on that of sight.

It may be remarked in passing that there is abundant evidence that the larvæ of these insects are infested by *Tachina*, and by hymenopterous parasites, and, as in other cases, probably these are really their most formidable enemies.

As to their enemies in the pupal state, there is no evidence. In the absence of such evidence it may be contended that any disquisition on the modes by which they may be protected from hypothetical enemies is premature. This, however, is a line of argument of which Mr Poulton and the apologists of Adaptation are well aware, and to which they expose themselves avowedly.

The fact, however, that the colour of these cocoons varies in accordance with that of adjacent substances did not seem, in my judgment, to be established beyond possibility of question, and it

was in the belief that some simple sources of error were not excluded that the following experiments were undertaken.

Eriogaster lanestris. I. A large colony of these caterpillars were brought home, they being then about three-quarters grown, and fed in a large plain glass vessel till Aug. 15. On that date the whole was examined, and 11 cocoons were found spun on leaves. Of these

6 were of full colour.
4 were dark, but not quite so full in colour.
1 was a good deal lighter, but still brown.

The dark colour is about the tint of black coffee, and the lighter specimen may be described as having the colour of strong tea with some milk in it. It will be convenient to refer to this specimen for comparison, and its tint may be spoken of as "half-colour."

II. From this colony a number were chosen which seemed to be ready to spin. These were shut up in a white muslin bag full of torn, crumpled strips of white paper. Of these larvæ several died, but five survived, and all spun cocoons attached to the muslin, or to the white paper, or to both. Of these five

3 were quite white.
2 were very pale cream-colour.

The paper and bag were bespattered with a brown juicy substance, which will be described later.

III. A number of apparently full-fed larvæ were similarly chosen and shut up in *dark* substances, and of these six survived and spun as follows:

(*a*) In black gauze, 1 specimen. Cocoon lighter than "half-colour."
(*b*) On brown paper in green muslin bag, 2 specimens. Both quite white.
(*c*) On brown dried leaves in a green muslin bag, 2 specimens. One white; one very pale cream-colour.
(*d*) In the same bag of leaves as (*c*); spun on the green muslin, 1 specimen. Cocoon white.

All these six cocoons, attached to dark substances, were of light colour. There was a good deal of brown evacuation, as in II.

IV. Two larvæ, which had begun to spin in leaves, were taken out and shut up in white paper. Both spun cocoons of light colour.

One larva, which had similarly begun to spin in a leaf, was taken out, and it eventually spun a white cocoon between green gauze and a piece of clear glass.

One larva, beginning to spin on white paper, was disturbed, and afterwards spun a white cocoon.

Therefore, of 4 larvæ which were disturbed while spinning, all spun light cocoons, 1 being on a dark substance, 3 being on white substances.

These results leave little room for doubt that the absence of colour in the cocoons results from an unnatural condition, such as disturbance at the time of spinning, or removal from food-plant when the growth is nearly complete. Besides these the presence of parasites should be mentioned as sometimes associated with a similar effect. This was seen once in a specimen of *E. lanestris*, and once in *S. carpini*, which were inhabited by a *Tachina*. In both these cases the cocoons were quite white. On the other hand, several *Tachinæ* were found in one *Saturnia* cocoon of *dark* colour. It will be seen, therefore, that though these observations fully confirm the statement that the larvæ do spin dark cocoons on the leaves, and white cocoons when confined in white paper, yet they suggest that the operating cause is the confinement and not the whiteness of the paper. The nature of the distinction between brown and white cocoons is discussed below.

V. From these experiments it appeared that light-coloured cocoons were produced when the larvæ were confined in white substances, and also when they were confined in dark substances, but that when left with their food the cocoons were dark. This result suggested that perhaps the alteration of colour was brought about by some unhealthy condition associated with the removal of the larvæ from their food. The four larvæ which had been disturbed whilst spinning also produced white cocoons, though one of them was attached to a dark object. From this it seemed likely that disturbance at the time of spinning might also be sufficient to prevent the cocoon from being properly coloured. It became therefore necessary to see what coloured cocoons would be spun by larvæ which of their own free will spun upon white paper. With this object the vessel in which the remaining larvæ were feeding was carefully filled with crumpled white paper, so that each twig of food (hawthorn) was more or less surrounded with paper. All the larvæ in this vessel chose to spin in the paper, and 14 cocoons were thus obtained. Of these 14 cocoons on white paper

4 were of full colour.

6 were lighter than this, but still substantially brown.

4 were light, 3 of them being white.

Of the 3 which were white, 1 was spun by one of 4 larvæ which remained at the last, and were not fed owing to a mistake.

To recapitulate: Of 11 larvæ left with their food, all spun dark cocoons on leaves.

Of 14 larvæ left with their food and white paper, 10 spun dark cocoons on white paper, and 4 spun light cocoons on white paper.

Of 11 larvæ which were shut up, all spun light cocoons, 5 being on white substances, and 6 being on dark substances.

Saturnia carpini. Eleven cocoons found spun in the hedges in a state of nature were all of full colour.

Experiments made with larvæ of this species agreed generally with the results from those made on *E. lanestris*, but I found it difficult to obtain any considerable number of dark cocoons from *carpini* larvæ in captivity, even when they were left with their food, and disturbed as little as possible.

Fifteen larvæ, which were shut up in various dark substances, such as brown paper, black muslin, green muslin, etc., spun cocoons which were all light in colour, though attached to dark substances, several being quite white. No dark cocoon was spun by any larva thus confined.

Fifteen larvæ were fed in a large vessel on food surrounded with crumpled white paper, treated as the *Eriogaster* larvæ were in Experiment V. Of these 15, only 7 spun dark cocoons; but of these, 3 were more or less attached to white paper, the remaining 4 being among leaves.

4 were light brown in colour, being attached to both twigs and paper.

4 were white or nearly so, being attached to paper and leaves.

From this it seems to be difficult to get conditions which are sufficiently healthy to enable the larvæ to spin dark cocoons, but it does not appear that the colour of the cocoons depends upon that of foreign substances.

Most of the bags and vessels in which the larvæ were confined were found to be bespattered with brown fluid similar to that which was seen in the case of the *Eriogaster*.

The colouring substance of the cocoons. It has been mentioned that many of the larvæ of *Eriogaster* and of *Saturnia* evacuated a quantity of brown fluid substance. The tint of this fluid so closely matches that of the brown cocoons that it seems possible that their colour may be given to them by an outpouring of the brown fluid upon them. In view of this possibility the nature of this fluid is a matter of interest,

and the following facts relating to it have a bearing on the question of the coloration of cocoons.

The brown fluid was found only in vessels in which large and presumably full-fed larvæ were living. In cases in which a larva was removed and shut up, it was generally present on the second or third day after removal, but there were several large patches of it in the large vessel in which the *Saturnia* larvæ were kept without disturbance. The fluid itself is viscous, and of a dark coffee-brown colour, closely resembling that of the cocoons. It generally contained some fœcal matter and particles of semi-digested food. From this, therefore, it may be concluded that the fluid is voided from the intestines, but I never saw a larva in the act of evacuating it. If this should be found to be the origin of the fluid, it may probably be looked on as being of the nature of "meconium."

The presumption that it is with this fluid that the cocoons are coloured rests on the following observations: A considerable number of larvæ, which were known to have voided the brown fluid, spun white cocoons. On the other hand, many spun white cocoons which were not known to have voided any fluid, though nevertheless they may have done so. Next, it was observed that some of the dark *Saturnia* cocoons, after they were just finished, were wet, as though drenched with brown fluid. Several also of the pale *Saturnia* cocoons had a darker patch in one part, generally upon the neck of the cocoon, though in one case there was a dark patch on the side. The appearance of these patches was exactly as if a quantity of brown fluid had been ejected upon the inside of the cocoon. In one case a brown cocoon of *Saturnia*, which was spun against a piece of white paper, lay on a large stain of the brown fluid; and there could be little doubt that the fluid had soaked through the cocoon on to the paper.

There is, then, good evidence that a brown meconial fluid is voided by caterpillars which are removed and shut up before they spin, and if it were to be established that the colouring matter of the cocoons is due, or largely due, to this fluid, the phenomenon of the colour-variation of cocoons becomes much simpler; for the cocoons of secluded larvæ are, on this hypothesis, white by reason of the previous voiding of the brown fluid, and the consequent absence of a supply of colouring matter.

It should be mentioned, as making against this view, that in the case of three *Eriogaster* larvæ, which were disturbed whilst spinning, and which afterwards spun white cocoons, it was almost certain that

no brown fluid was previously voided. It is, of course, possible that the shock of disturbance may have led to a retention of the brown fluid, though this cannot be proved.

After these experiments were performed I received information that Mr Poulton[1] and Prof. Meldola have shown that the cocoon of *Eriogaster* is largely made up of oxalate of lime, which is deposited on the first thin web of silk. There was no direct evidence as to the manner in which this substance is deposited, but it was believed to be voided from the intestine. This observation would thus to some extent give support to the suggestion here made, that the colouring matter of the cocoons is produced chiefly, if not altogether, from the intestine.

[1] In a paper read before the Physiological Society, not yet published (February, 1892).

VARIATION IN THE COLOUR OF COCOONS, PUPÆ, AND LARVÆ: FURTHER EXPERIMENTS

[*Trans. Ent. Soc. Lond.*, 1892]

I. *The Colour of the Cocoons of* Saturnia carpini

In the *Trans. Ent. Soc. Lond.* 1892, Part 1, p. 45, I gave an account of some experiments touching the variation of the colour of the cocoons of the small egger (*Eriogaster lanestris*), and of the emperor moth (*Saturnia carpini*). It has been stated by Poulton[1] and others that the familiar variation of these cocoons, from coffee-brown to a cream-white colour, takes place in accordance with the substances to which the cocoons are attached, and the inference was suggested that this variation in colour was a protective adaptation to render the cocoons inconspicuous. The evidence which I brought forward went to show that the statement that there is any relation between the colour of these cocoons, and that of the substances to which they are attached, was founded on a mistake. In the case of *Eriogaster*, experiment showed

(1) That caterpillars left to spin in the leaves of the food-plant (hawthorn) spin *dark* cocoons.

(2) That caterpillars taken away from their food and shut up spin *light* cocoons, whether the surroundings in which they are confined are black or white.

(3) That caterpillars which of their own choice crawl into and spin in white paper placed amongst their leaves spin *dark* cocoons.

From these results it was to be concluded that the cause determining the production of light cocoons was removal from the food, or the state of annoyance incident to such removal, and that in fact the light-coloured cocoon was an abnormal product resulting from unhealthy conditions.

As regards *S. carpini*, of the three points given above the second was fully established. No caterpillar which was removed and shut up spun a dark cocoon. The other two points were not fully established, for, while all the cocoons which I could find wild in the hedges were dark, few comparatively of those fed in captivity spun cocoons of full colour. Several of these, however, were attached to white paper, as in (3).

Lastly, in the case both of *Eriogaster* and *S. carpini*, there was

[1] E. B. Poulton, *Colours of Animals*, pp. 142–146.

evidence to show a strong probability that the colouring matter was derived from the contents of the alimentary canal, and that in the case of the light cocoons this substance was either evacuated, or not produced, or possibly absorbed. Two points, therefore, remained for further investigation; first, whether *S. carpini*, if in healthy circumstances, will spin dark cocoons independently of the colour of its surroundings; and secondly, the far more important question of the nature and origin of the colouring substance. To the solutions of both of these questions the evidence to be given contributes.

(1) From two batches of eggs I reared about 140 larvæ of *S. carpini*. Supposing that my larvæ had not been under good conditions last year, I resolved this year to sleeve them on a bush in the open air. On July 2, therefore, when they had made their last moult, I divided them into two lots, A and B.

A. Sixty-six larvæ were placed on a large branch of hawthorn in the Botanic Garden, and were covered with a large sleeve of white muslin. Into this sleeve I put a considerable quantity of crumpled white paper, arranging it so that the paper lay thickly amongst the leaves. In the autumn, when all had spun, I opened the sleeve, and counted the cocoons, numbering 53, the remainder having presumably escaped. Of these:

7 were spun on the white sleeve.

18 were spun in the white paper, or between it and the sleeve.

19 were spun partially attached to the white paper and partly to twigs, etc.

9 were spun on leaves or twigs, not attached to the white paper or sleeve.

With one exception all these cocoons are of the full dark colour. The exception is also a brown cocoon, but it is very thin and deficient in substance, and consequently of rather a lighter colour. It is one of the 19 named above.

B. Forty-four larvæ were enclosed in a sleeve of black muslin, and placed on another branch of the same bush. Into this sleeve I put a quantity of crumpled brown paper, of the darkest colour I could get. On opening this sleeve in September, I found 38 cocoons, namely:

2 in brown paper.

1 between paper and leaves.

4 on the black sleeve.

31 in the leaves, or massed against each other.

All these were of the full dark colour. I should say that the brown paper had become so much bleached by exposure to weather that it could scarcely be called brown.

This experiment must, I think, be considered to show conclusively that there is no relation between the colour of the cocoons of *S. carpini* and that of the substances to which they are attached. We need not therefore, in this case, consider the difficult problem whether, if such a relation did exist, it might or might not be properly considered a protective device.

(2) As to the origin of the colouring substance, I have satisfied myself that it is obtained from the contents of the alimentary canal. This conclusion is made for the following reasons:

(*a*) The white cocoons are thin and papery, while the dark cocoons are stiff and very shiny, on the inside especially, looking as if they had been stiffened with brown size.

(*b*) In the case of some brown cocoons spun against white paper, there was a brown stain on the paper, as though a brown fluid had oozed through.

(*c*) In the case of a majority of larvæ, which, in 1891, spun white cocoons, there was evidence to show that an evacuation of the contents of the alimentary canal had taken place.

(*d*) This evacuation is, when still wet, of a reddish brown colour, of a viscous consistency, and contains small pieces of chewed leaves, and sometimes half-formed fæces.

(*e*) On opening a larva, whether young or nearly full-fed, the contents of the alimentary canal are bright green, but upon exposure to the air they turn to the red-brown colour of the evacuations seen in the breeding-cages. By washing out the contents of the alimentary canal, and filtering out the *débris* of food, a clear green filtrate was produced, which turned red-brown in the course of some minutes. There can be no doubt that this change is connected with oxidation, for it takes place more rapidly if the test-tube containing the fluid is shaken, and immediately if yellow nitric acid is added. Moreover, if the contents of the alimentary canal are placed on a glass plate, the surface soon turns in colour, while the lower part next the plate may be seen to be still green. The change from green to red therefore results from oxidation.

The actual origin of this colouring matter in the alimentary canal is not easy to determine. There are two chief possibilities; first, that the green colour is a substance (such as bile, for example) secreted by

the animal; or, secondly, that it is formed from the food. The first of these is almost certainly disproved by the fact that there is no green substance in the walls of the gut, or in the tissue adjacent to it, which undergoes the change described; whereas, if the substance were the result of secretion, it would be expected that this would be the case. Filling the tissue-spaces surrounding the gut there is indeed a green fluid, but this retains its colour on exposure unchanged, not even turning to black, as do the body-cavity fluids of so many larvæ.

If, then, the colouring substance is not a secreted body, but is formed in some way by digestion from the food, the question naturally suggests itself, is it a chlorophyll product? That this is so is on the whole likely, but I know no way by which it might be proved to be so. For since the whole gut is filled with chewed leaves, there is of necessity much chlorophyll present, and it is not possible to obtain the colouring substance free from chlorophyll.

In this connection it should be remembered that the brown colour of the cocoons is a very good match with the brown to which hawthorn leaves turn in winter, and it is not unlikely that the change from green to brown undergone by the colouring substance of the cocoons may be akin to that which takes place in the leaves. This suggestion is, of course, merely made for what it is worth.

If the contents of the gut are dried, the brown substance remains perfectly soluble in water.

(*f*) The proof that the green colouring matter from the gut is used to dye the cocoon brown rests on the following observations: If a larva is irritated it ejects from the mouth a green glairy fluid, which turns red-brown, like the contents of the gut. If a piece of a *white* cocoon be laid in this fluid for some minutes, it soon acquires the brown colour of a brown cocoon, from which it is indistinguishable. The same is true of a fibre of silk drawn from a spinning animal, which can be dyed in the same way. The colour is then insoluble, and cannot be washed out, having stained the silk like a mordant. In the previous experiments, in 1891, I was puzzled by finding the colour soluble in the evacuations, but insoluble in the cocoons; but this is no doubt the explanation.

(*g*) Lastly, it is to be considered how the colour gets from the animal's gut to the silk. As to this, I have no decisive evidence. I know that a caterpillar may spin brown threads without touching them with the posterior end of the body, and it is therefore clear that the colour may be given out from the mouth, just as it is when the

larva is irritated. But the appearance of the interior of a cocoon rather suggests that a large quantity of the size-like matter has been poured out at once. It seems possible, therefore, that there may be a final discharge from the intestine after the cocoon is finished. I am inclined to think that some of the threads are often spun white, and smeared with the colour afterwards, for I have seen threads of a cocoon lately begun, first white and then brown after an absence of an hour, and the animal may often be seen, as it were, "mouthing" over its threads. This is not always the case, for I have seen very dark threads lying adherent to the surface of paper, in such a position that they could not have been gone over again without staining the paper, but must have been put down brown while still viscous.

I think, then, it may be safely concluded (1), that the brown colour of the cocoons is derived from the alimentary canal; (2), that it is produced in the digestion of the food, and that it is *probably* a chlorophyll-derivative; (3), that it is imparted to the silk from the mouth of the larva, and perhaps by evacuation from the intestine also.

I have to thank Dr A. Sheridan Lea for kindly advising me in the examination of this substance.

II. *The Colours of Pupæ of* Vanessa urticæ

The pupæ of *V. urticæ* and of some other butterflies are known to be sometimes much pigmented, and sometimes very light, with little or no pigment. Apart from the pigmentation, they also vary greatly in the extent and brightness of the metallic lustre, which is so marked a feature of these forms. Poulton[1] has described experiments showing that there is a relation between these variations and the colours of the linings of the cages in which the larvæ pupated. In the past summer I made experiments of the same kind on *V. urticæ*, and the results fully bore out Poulton's account, to which I can add little.

The larvæ were collected when about half-grown, and were put into shallow cardboard boxes, through one end of which the stem of a nettle was passed. The boxes were lined with one or other of the following papers: (1) gilt, (2) silver, (3) yellow, (4) white, (5) black, or (6) painted with Indian ink. The face of each box was covered with a pane of glass, and the boxes were all placed upright in a row facing a south window. During the three weeks through which the experiments continued there was generally a bright sun, so that the boxes became very hot. In some of them there was a good ventilation

[1] E. B. Poulton, *Phil. Trans.* 1887, vol. CLXXVIII, B, p. 311.

maintained, while others were kept very close, so that by the transpiration from the plant the atmosphere of the box was saturated with moisture, which also trickled continually down the glass. I did not find that the condition of moisture or dryness affected the colours of the pupæ. It is perhaps unnecessary that these experiments should be described in detail, as Poulton's description is complete.

One series of experiments, made by way of control, have, however, some interest, as materially confirming the view that the change in the colours is really due to the action of light. A number of larvæ were shut in gilt boxes as described, and these were immediately placed in a dark, closed cupboard, which was not opened again until the larvæ had pupated. With few exceptions all these pupæ belonged to the darkest class (see table). Other larvæ were put in a black box and similarly treated, with the same result.

The larvæ were collected from various places round Cambridge, and belonged to some dozen or more batches of larvæ, but I distributed the families among the boxes so as to test the existence of any congenital differences as regards pupal colour, but found none.

Some interest attaches to the fact that the great proportion of larvæ collected by me were infested with *Tachinæ*. Probably, in round numbers, five or six larvæ died from *Tachina* for one that pupated, but those that did pupate almost without exception emerged. There is therefore no reason to suppose that either the gilt pupæ or the dark ones are diseased.

	Much Pigment			Some Pigment			Little or no Pigment		
Amount of Gilding	None	Some	Much	None	Some	Much	None	Some	Much
Gold paper . .		2		2	5	9		9	14
Silver do. . . .				2	2			2	3
White do. . .				4				2	2
Yellow do. . .					1				5
Black do. . . .	9	5			1	1			
Indian Ink . .	10	6	1	2	3		1	2	
Shut in the dark:									
Gold	26	3			1				
Black	9								

Taken together—gold, silver, yellow, and white papers gave 2 dark, 25 moderate, 37 light; black paper and Indian ink gave 31 dark, 7 moderate, 3 light; gilt paper, shut in the dark, gave 29 dark, 1 moderate; black paper, shut in the dark, gave 9 dark.

There are, of course, two things to be thought of: first, the pigmentation; secondly, the metallic colours. As the table shows, both these

qualities seem to be affected by the surroundings. As Poulton has mentioned, the metallic appearance is an interference-colour, disappearing when the pupæ are dried, returning when they are wetted. Of the physiology of these phenomena I have gleaned no hint at all.

The whole question touching the putative utility of these colours as a protection seems to me an unprofitable field for study. As to the enemies of these creatures, other than insect-parasites, there is almost no evidence, and as to the senses by means of which these parasites seek their prey, there is still less. Of enemies to any of these forms in the pupal state, there is, so far as I know, no direct evidence at all. The pupal state is very short, lasting about a fortnight or three weeks, according to the weather, and the view that these peculiar colours have been developed by these creatures to conceal them from imaginary enemies during that brief time is, in my judgment, quite unsupported by fact. This view is applied to the case of these pupæ by an indiscriminate extension of deductions made in other cases fairly enough, as, for example, in that of the larvæ of *A. betularia* (*v. infra*).

After experience of these pupæ, the doubt whether the metallic colour can in any way lead to their concealment is stronger than it was. The gilded pupæ, so far as I can see, do not by reason of their gilding approximate to the appearance of any natural substance, either of flakes of mica, or to the dried slime left by slugs, or to any other bright objects to which they have been compared by ingenious persons. If Mr Poulton had spoken of this gilding as a "warning coloration," I should have been less surprised.

One thing more may be said. In the case of the sole, in the case of the larvæ of *A. betularia*, and the like, there can be no doubt that the change of colour represents an "attempt" on the part of the animal to approximate to the colour of its surroundings. Now, in the case of these gilt pupæ, do we really know that the change represents any such effort at approximation? I confess that, though as regards the deposit of pigment this may be so regarded, the change in the degree of metallic colouring does not seem to me to be an approximation of this kind at all. It is true that gilt paper makes some approach to the look of these pupæ, but the yellow paper, and silver or white papers, do not in the least. In this connection a circumstance, which I saw several times, may be mentioned. In several cases a larva in a gilt box pupated, not on the gilt paper, but on leaves of the

food-plant, so that it was not anywhere exposed to the paper; sometimes, indeed, when practically surrounded by a leaf or leaves, and among these were some of the most golden pupæ. Notwithstanding, therefore, the clear evidence that the proximity of brightly illuminated surfaces promotes the production of the metallic appearance in these pupæ, I cannot see that there is any reason to suppose that this is a "protective resemblance," or, indeed, that it is a "resemblance" at all.

In his work on this subject, Mr Poulton indeed admits that by reason of their metallic lustre the pupæ do not resemble any substance to which they are attached in nature; but he suggests that perhaps they may have come through a phylogenetic phase in which they did attach themselves to such substances. Though nothing forbids anyone from framing such an hypothesis, it is surely evident that if conjectures of this kind are to be admitted as a basis for argument, all zoological science will be thrown into confusion.

III. *The Colours of Larvæ of* Amphidasys betularia (*the Pepper Moth*)

Mr Poulton was kind enough to send me some newly-hatched larvæ of *A. betularia*, with the suggestion that I should repeat his interesting experiment described in *The Colours of Animals*, 1890, pp. 152 and 153. Larvæ reared among green leaves and green twigs only were said to be green through life, while larvæ reared on leaves amongst which darkly coloured sticks were placed were stated to assume a dark colour.

My experiment has substantially verified Mr Poulton's account. When the larvæ came to me they were of a kind of medium brownish green colour, being rather more brown than green. They were divided into four lots on July 12.

Two lots (A) were fed on green leaves (*Populus nigra*) without black sticks, and two lots (B) were fed on green leaves amongst which black sticks were placed. Care was taken that the leaves given to all were from shoots of similar age.

It is scarcely necessary to describe the course of the experiment in detail, as Mr Poulton has already done so; but I may give the conditions seen at two examinations:

July 24. *Lot A*. Originally 13. Of these 8 were of the full bright green colour, 2 were brown-green, and 2 were brown.

Lot B. Originally 14. Of these 12 were very dark in colour, 1 was green, and 1 was dead.

I then took all the sticks out from among the B lot, and put them with Lot A. On August 7, the result was as follows:

Lot A. 7 very green, 2 medium brownish green, 1 darker, but not of the full dark colour; 2 dead.

Lot B. 12 still very dark, 1 green as before.

No further change in colour took place, so far as I could judge. The effect therefore, once produced, seems not to be reversible, as it is in the case of the sole and the like. The change of colour is, as Poulton says, produced by the deposit of dark pigment in the one set of larvæ, and by the absence of it in the other.

It should be mentioned that these larvæ, like many other *Geometræ*, are almost exclusively night-feeders, and rarely move by day. Those provided with black sticks sat *either* on them or on the green twigs of their food throughout the day. Of course, in this case the resemblance to sticks in the one case and to green twigs in the other is unquestionable, and I think it may be fairly argued that this resemblance may contribute to the protection of the animal.

My best thanks are due to Mr Poulton for giving me an opportunity of making this experiment, which I have watched with great interest.

NUMERICAL VARIATION IN TEETH

[*Proceedings of the Zoological Society*, 1892]

THE following paper is an abstract of facts regarding the Numerical Variation of Teeth and of certain conclusions as to the nature of the conception of Homology as applied to Teeth which those facts have suggested. The observations concerning teeth form part of an investigation of the Variation of Multiple Parts in general, and I hope that before long the results of this work will be published in a complete form by Messrs Macmillan, to whom I am much indebted for leave to use the blocks with which this paper is illustrated.

In an abstract it is clearly impossible to set forth the precise value and significance of the study of Variation as a clue to the problems of Descent; but since by most this subject is wholly neglected, it may be well to state in the fewest words why it is that this method of investigation is not merely a good one, but perhaps the best open to us.

The reason, then, is this. We assume that the transition from one form to another takes place by Variation. If, therefore, we can see the variations, we shall see the precise mode by which Descent is effected. Now the problem of Descent includes the problem of Homology, and, therefore, in any case of supposed Homology between organs the ideally best proof or disproof of such a supposition is to be had by appeal to the facts of Variation. For the statement that an organ of one form is homologous with the organ of another form means that there is between the two some connection of Descent, and that the one organ has been formed by modification of the other or both by modification of a third. The precise way in which this connection exists is not defined, and, indeed, has scarcely ever been considered, and though such a consideration must be hereafter attempted, the matter cannot be discussed here. We must be content for the present with the belief that in some undefined way there is a relationship between homologous parts, and that this is what we mean when we affirm that they are homologous. In the case of the homologies of Teeth, we are concerned with the application of this belief or principle to the case, not of a single organ, but to Multiple Parts arranged in series. If, then, the whole series of teeth in one form is homologous with the whole series in another, we have now to consider how far we can extend the principle to the case of individual

members of the two series. This is the question which is again and again arising with regard to Multiple Parts, but there are still no general principles by which it may be decided.

But though no one has told us the steps by which the Numerical Variation of Teeth proceeds, there is nevertheless a received view by which it is sought to interpret the phenomena, and though there are several schemes upon which the homologies of teeth are defined, all are alike based upon one principle, which may be stated as follows.

It is believed that in the case of mammals, perhaps excluding the Cetacea, the series of teeth consisted originally of some maximum number from which the formulæ now characteristic of the several forms have been derived by successive diminution. On this view the series is believed to be always *composed of definite and individual members, which in any given form are either present or absent*; and the business of the homologist is then to determine which in each case is present and which absent. This hypothesis, of course, involves a definite conception of the mode in which Variation works, and it is most important to realise this clearly. For if it is true that each member of the Series of Teeth has in every form an individual and proper history, it follows that if we had before us the whole series of ancestors from which the form has sprung, we should then be able to see the history of each tooth distinctly and severally in the jaws of each of these progenitors. In such a series the rise of one individual tooth and the decline of another would then be manifest. Each would then have its individual history, just as a Fellowship of a College or a Canonry of a Cathedral has an individual history, being handed on from one holder to his successors, some being suppressed and others being founded, but none being merged into a common fund. In other words, the received view of the nature of homologies in teeth *assumes that in Variation the individuality of each member of the series is respected.*

The difficulty in applying this principle is notorious, not only in the case of teeth but in all cases of Multiple Parts, such as digits, phalanges, etc.; and when the actual evidence of Variation is before us, the cause of this difficulty will become apparent enough, for it will be found that though Variation may sometimes respect the individual homologies, yet this is by no means a universal rule; and, as a matter of fact, in all cases of Multiple Parts, as to the Variation of which any considerable body of evidence has been collected, there are numerous

instances of new forms arising in which what may be called the stereotyped or traditional individuality of the members has been superseded.

The present paper concerns the case of Teeth only, and even of this part of the evidence only a fragment can be given in this abstract, but perhaps it may suffice at least to indicate some of the possibilities which are opened up by the study of Variation.

The material examined has consisted chiefly of specimens in the British Museum and the Museums of the College of Surgeons, Leyden, Oxford, and Cambridge, the Paris Museum of Natural History, and several smaller collections. I have to thank the authorities of these several museums for the great kindness I have received from them in the course of my work; and in particular I must express my indebtedness to Mr Oldfield Thomas, of the British Museum, for the constant help and advice which he has given me, both as regards the subject of teeth generally, and especially in examining the specimens in the British Museum.

For various reasons I have for the most part limited myself to the following groups: Primates (excepting Lemuroidea), Carnivora (Canidæ, Felidæ, Viverridæ, Mustelidæ, and Phocidæ), Marsupialia (Phalangeridæ, Dasyuridæ, Didelphyidæ, part of Macropodidæ, etc.).

Except in the case of teeth which are the terminal members of series, such as the first premolar or the last molar, very few facts of importance concerning the process of reduction in number were seen. From the fact that such cases are generally more or less ambiguous, they must be reserved for fuller treatment. For the present it must suffice to give a brief account of some of the more remarkable phenomena relating to increase in number of teeth.

The statistics relate to about 2500 skulls belonging to various orders, and the comparative frequency of supernumerary teeth in some of the different groups is interesting if only from its paradoxical character.

Primates. Of the three larger Anthropoids—Orang, Chimpanzee, and Gorilla—141 normal skulls were seen, and 11 cases of supernumerary teeth, or nearly 8 per cent. (in addition to 7 recorded cases known to me). On the other hand, no case was seen in 51 skulls of *Hylobates*, which were all normal. And of Old World Monkeys other than these, I found only two cases in 423 skulls, or less than ·5 per cent.

In the species of Cebidæ and in *Ateles* supernumerary teeth are common, five cases being found in 131 skulls, or nearly 4 per cent. (in addition to 4 recorded cases); while in 92 skulls of other New World Monkeys there was not one case.

Phocidæ. 139 normals, 11 cases of supernumerary teeth, or 7·5 per cent.

Otariidæ. 121 normals, 5 cases of supernumerary teeth, or 4 per cent.

Canidæ. Of *wild* Canidæ, 289 normals were seen, and 9 cases of supernumerary teeth, or 3 per cent. (in addition to numerous recorded cases).

Of domestic Dogs, including Pariahs, etc., 200 skulls were normal and 16 had supernumerary teeth, or 8 per cent. (besides many recorded cases).

Felidæ. Of *wild* Felidæ, 278 normals and 6 cases of supernumerary teeth, or more than 2 per cent.

Of domestic Cats, 35 normal and 3 cases of supernumerary teeth, or 9 per cent.

Viverridæ. 94 normals (not regarding variation affecting the first premolar only) and 4 cases of supernumerary teeth.

Owing to the great variability of the dentition of some groups of Marsupials and the difficulty of deciding on the normal formula, it would not be profitable to give summary statistics which should be satisfactory.

It will be seen that, so far as the statistics go, supernumerary teeth were more common in domestic Dogs than in wild Canidæ, and though the number of Cats seen was small, the same is true in their case also as compared with wild Felidæ. But though it is received by many almost as an axiom that domestic animals are, as such, more variable than wild ones, and though the figures somewhat support this view, it is necessary to point out that such a deduction should be made with great caution. For while it is true that the domestic Dog is more variable in its dentition than wild Dogs, it is not true that it is much more variable than many other wild animals, as, for example, the Anthropoid Apes, some of the Phocidæ, several genera of Marsupials, and others. The doctrine that domestication induces or causes Variation is one which will not, I think, be maintained in the light of fuller evidence as to the Variation of wild animals. It has been suggested by the circumstance that so many of our domesticated animals are variable forms, and that so little heed has been paid to the variation

of wild forms. To obtain any just view of the matter, the case of variable domestic species should be compared with a species which is variable though wild. The case of the great variability of the teeth of the large Anthropoids, which is shown not merely in numerical changes, but in frequent abnormalities of position and arrangement, is most striking, both when it is compared with the great rarity of variations in the teeth of the Old World Monkeys and the *comparative* rarity of great variations even in Man. If the Seals or the Anthropoids had happened to be domesticated animals, I do not doubt that many persons would have seen in this variability a consequence of domestication. When the whole evidence is examined, it will be found that we can make no generalisations of this kind, and that the variability of a form is, so far as can be seen, as much a part of its specific characters as any other feature of its organisation. A few curious cases may be given in illustration. Of *Canis cancrivorus*, a S. American Fox, I know the following specimens only (in the British Museum)—normals (numerically): one whole skull with lower jaw, one skull without lower jaw, and one lower jaw without a skull, and in one of these right $\overline{m^3}$ is much larger than the corresponding left tooth; abnormals: two skulls have $\overline{m^4}$ on both sides, and a third has a large "odontome" formed as 4 small molars growing from right $\overline{m^3}$. Of *Felis fontanieri*, an aberrant Leopard, two skulls only are known (British Museum), and both of these show dental abnormalities, one having supernumerary left $\overline{m^2}$, and the other having an additional talon to right $\overline{p^3}$, making it almost a "bigeminous" tooth. In the Seals only three cases of reduplication of the first premolar were seen, and two of these were in *Cystophora cristata* (Leyden and Cambridge). Evidence of this kind might be multiplied indefinitely.

The following cases are chosen as representative examples or "Prerogative Instances" of different classes of phenomena which occur in connection with increase in number of teeth. It will be understood that the cases are selected as illustrations, and that in order to have a full appreciation of their significance, the whole body of evidence must be taken together, for scarcely any two cases are exactly alike.

Division of Individual Teeth

Ommatophoca rossii. Of this form two skulls only are known, namely, those in the British Museum. One of them has the arrangement usually found in Phocidæ, viz., five teeth behind the canines,

giving the formula: i. $\frac{2-2}{2-2}$, c. $\frac{1-1}{1-1}$, p. + m. $\frac{5-5}{5-5}$. By the analogy of other Seals, these five teeth are p. $\frac{4}{4}$, m. $\frac{1}{1}$. The other specimen is exceedingly remarkable (Fig. 1). In it the incisors and the canines are the same as in the first specimen, but the first tooth behind the canine on both sides in the lower jaw and on the right side in the upper jaw has a very peculiar form, having a deep groove passing over the whole length of the tooth on both its outer and inner sides. These grooves

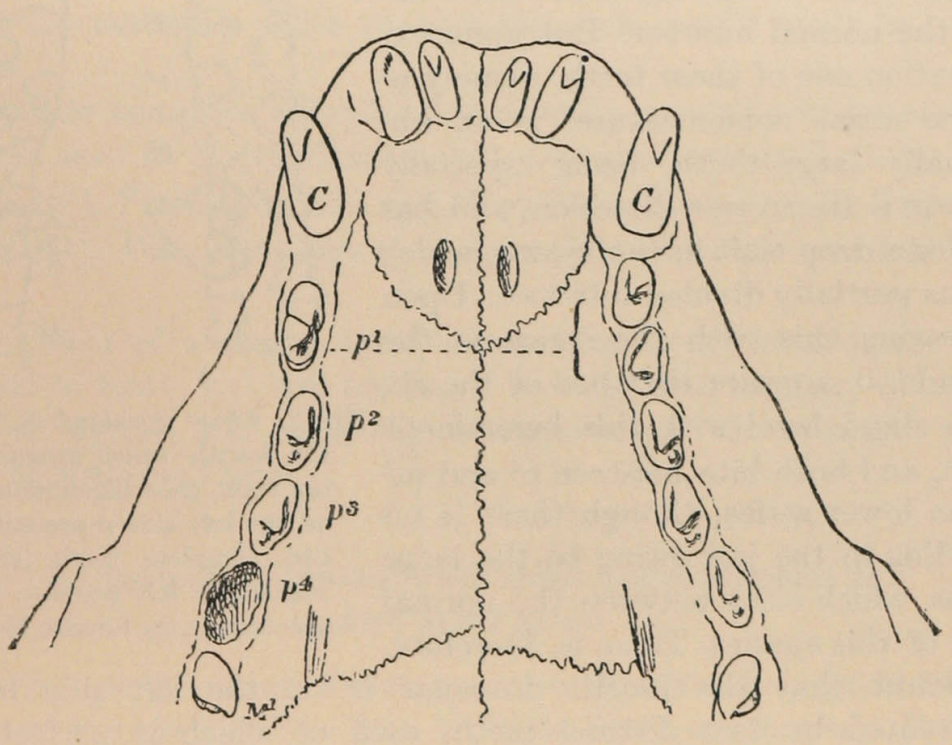


Fig. 1. *Ommatophoca rossii*, having the first upper premolar on the right side bigeminous, and on the left side represented by two complete and similar teeth. In the lower series the first premolar was bigeminous on both sides. From a specimen in the British Museum.

extend from the tip of the root along both sides of the crown, and thus imperfectly divide each tooth into an anterior and a posterior half. The cusp of each tooth is also divided by the grooves so as to form two small cusps. Each of these teeth is therefore an imperfectly double structure, and may be described as being just halfway between a single tooth and two teeth.

On the left side in the upper series, as the *vis-à-vis* to one of these double teeth, there are two complete teeth, standing near together, but having separate sockets divided from each other by a bridge of bone. The dental formula for this skull taken as it stands is: i. $\frac{2-2}{2-2}$,

c. $\frac{1-1}{1-1}$, p. + m. $\frac{5-6}{5-5}$, for since the bigeminous teeth are not completely divided into two, they must be reckoned as single teeth.

Phoca grœnlandica. A specimen is preserved in the Leyden Museum having the arrangement shown in the figure (Fig. 2)[1]. The dentition of the lower jaw is the same on both sides. In the upper jaw there are on the left side *six* teeth behind the canine, while on the right side there are *five*, the normal number. But upon examination one of these teeth, namely $\overline{p^4}$ of the usual nomenclature, is an abnormally large tooth, being especially thick in a transverse direction, and has besides a deep cleft in the crown, which is thus partially divided into two. Upon comparing this with the series on the left side, it appears that *two* of the six teeth stand level with this bigeminous tooth, and both bite between $\overline{p^4}$ and $\overline{m^1}$ of the lower series, though there is no crowding in the jaw owing to the large spaces which exist between the normal teeth of this species. There is, therefore, no doubt that the fourth premolar is on the left side bodily represented by two distinct teeth, each of which is perfect and complete, while on the right side the process of division is incomplete.

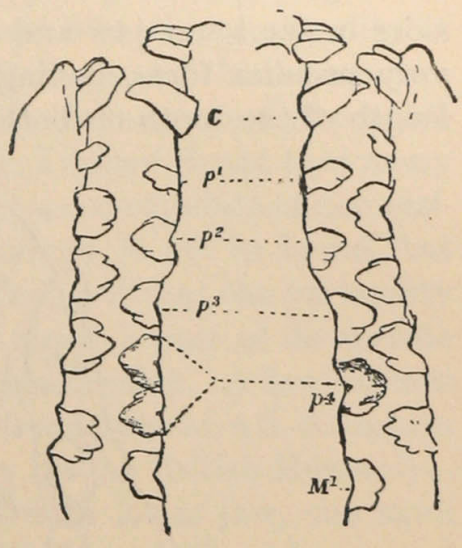


Fig. 2. *Phoca grœnlandica*, having the fourth upper premolar on the right side bigeminous, and on the left side represented by two complete teeth (shaded). Right and left profiles; from a specimen in the Leyden Museum.

In the Paris Museum (A 2897) there is a specimen of *P. grœnlandica* in which the second upper right premolar is represented by two teeth, each of which has two roots; but these two teeth stand at the same level in the arcade, one being external and the other internal. On the left side the second upper premolar is incompletely double, the crown being divided by an oblique constriction into an anterior and internal portion and a larger posterior and external part. The former has one root and the latter has two.

It is thus seen that reduplication of teeth may occur in such a way that a tooth which is normally single may be represented by two teeth, and that the two teeth thus formed may either (1) both take

[1] This figure was kindly drawn for me by Mr J. J. Lister.

places in the ordinary series, or (2) may stand externally and internally respectively.

Substitution of two teeth for one, both being in series, was seen in *Ommatophoca rossii* ($\underline{p^1}$), *Phoca grœnlandica* ($\underline{p^4}$), *Otaria ursina* ($\underline{p^2}$), *Brachyteles hemidactylus* ($\underline{p^1}$), *Phalanger orientalis* ($\underline{p^1}$), ditto ($\underline{p^3}$), *Myrmecobius fasciatus* ($\overline{i^3}$), ditto ($\overline{i^4}$). Probably also cases of the presence of two similar small teeth in place of the first premolar in the Canidæ and Felidæ should be looked on as belonging to this class, though the materials which support this view cannot easily be given in brief.

Partial or complete reduplication of teeth occurring in the second way was seen in *P. grœnlandica* ($\underline{p^2}$), *Otaria cinerea* ($\underline{m^1}$), *Canis mesomelas* ($\underline{p^3}$), *Vison horsfieldii* ($\overline{p^4}$), *Herpestes orientalis* ($\underline{p^2}$), *Herpestes gracilis* ($\overline{p^3}$), *Felis domestica* ($\underline{p^4}$), ditto ($\overline{p^3}$), *Phalanger orientalis* ($\underline{i^3}$), etc.

The power of a single organ to reproduce itself is of course not confined to teeth, but will be shown to be present in many different kinds of organs, and especially in those which are arranged as a Series of Multiple Parts.

Variation in Terminal Teeth when a New Member is added to the Series

This is a phenomenon which is most instructive as a guide to the nature of the process by which Multiple Parts are formed. It may be stated generally that if the tooth which is the last of a normal series is relatively a small tooth, as, for example, $\overline{m^3}$ or $\underline{m^2}$ in the Dog, then in cases of an addition to the series by which this terminal tooth becomes the penultimate it will be found that this penultimate tooth is larger and better developed than the corresponding ultimate tooth of a normal animal of the same size. Of this phenomenon two examples must here suffice.

The first is a skull of *Canis azaræ* in the Leyden Museum (Fig. 3, p. 186)[1]. In this figure, I and II represent the back-teeth of this abnormal specimen, I being the upper, and II the lower jaw. By the side of these are shown the upper and lower jaws of a normal specimen of rather larger absolute size. In the upper jaw there is a supernumerary m^3 on both sides and the great enlargement in m^1 and

[1] This drawing was kindly made for me by Mr J. J. Lister.

especially in m^3 is very striking. In the lower jaw there is no extra tooth, but the molars are considerably larger than the normal size.

The next case is that of *Dasyurus maculatus*, having an extra molar in the left upper and both lower jaws. In this case, owing to the great difference which normally exists both in shape and size between the last tooth and the last but one, some obscurity is introduced by the changes associated with the presence of an extra tooth,

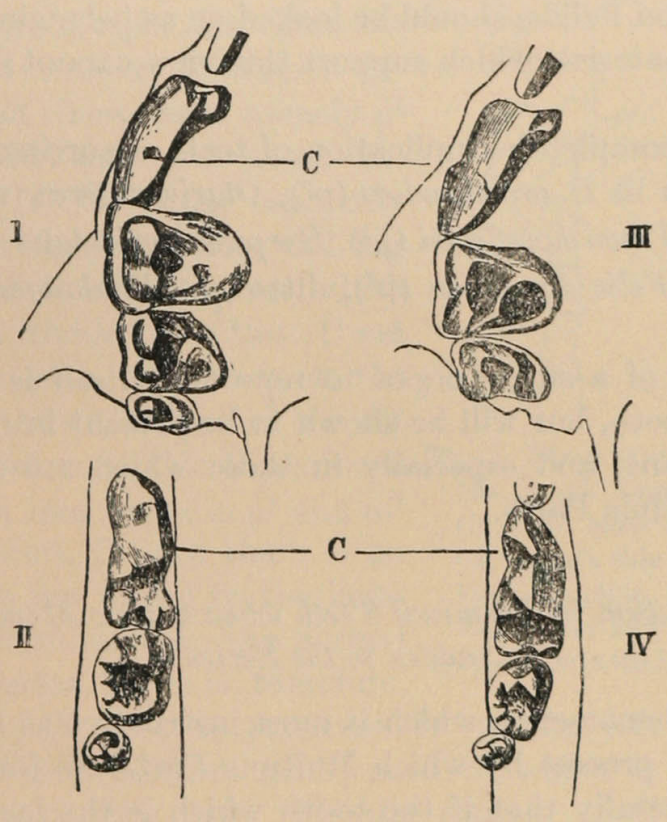


Fig. 3. *Canis azaræ*. I. Right upper molars of a specimen having a supernumerary third molar on each side. II. The right lower jaw of the same. III and IV. The right upper and lower jaws of a normal skull of rather larger absolute size, to show the increased size of the teeth in the abnormal specimen. C. The carnassial tooth. From specimens in the Leyden Museum.

and it would be difficult to determine the nature of the upper teeth if this phenomenon of Variation were unrecognised. The structures are shown in Fig. 4, A being the right upper jaw of a normal specimen, while B and C are the jaws of the abnormal form (Brit. Mus. 983 *b*). The normal specimen is unfortunately much larger than the other, which Mr Thomas tells me is abnormally small for the species. In the upper jaw of a normal skull there are two small premolars (p^1 and p^3 of Thomas) and behind these four molars. The molars increase in size from the first to the third, which is by far the largest. Behind

the third is the fourth molar, which is much thinner than the others. On comparing the abnormal skull with the normal one it is seen, firstly, that on the left side there are seven teeth behind the canine, while on the right side there are only six such teeth, as usual. On the right side, however, the last molar has not the thin flattened form of the last molar of a normal skull, but is a fair-sized thick tooth. In each lower jaw there are seven back-teeth instead of six. In making a more detailed comparison, the first five teeth on each side are clearly alike, while from its form the seventh on the left side might be thought to represent the normal sixth, and this is the view originally proposed by Mr Thomas in his *Catalogue of Marsupialia*, p. 265, *note*. The

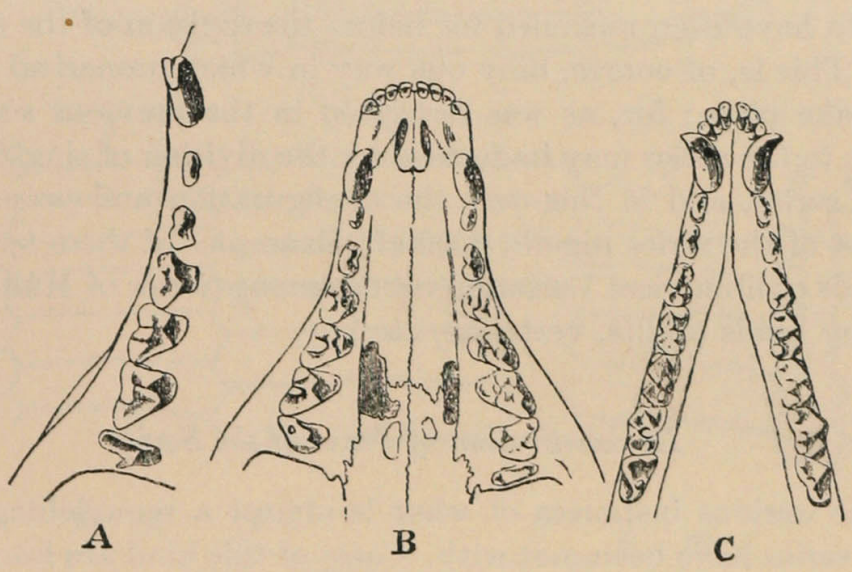


Fig. 4. *Dasyurus maculatus*. A, right upper jaw of a normal specimen. B and C, upper and lower jaws of an abnormal specimen having an extra molar in each lower jaw and in the left upper jaw. In correlation with this change the sixth upper back-tooth (m^3) has been increased in size. (The abnormal specimen was of less than normal size.) From specimens in the British Museum.

difficulty in this view is that it offers no suggestion as to the nature of the sixth tooth on the right side. In the light, however, of what has been observed in other cases of extra molars, it seems likely that on the right side m^4 has been raised from a small tooth to one of fair size, while on the left side the process has gone further, m^4 being still larger and another tooth having been formed behind it. Mr Thomas, to whom I am greatly indebted for having first shown me this specimen, allows me to say that he is prepared to accept the view here suggested.

This phenomenon, of the enlargement of the terminal member of a series when it becomes the penultimate, is not by any means confined to teeth, for the same is true in the case of ribs, digits, etc.,

and it is possibly a regular property of the Variation of Series of Multiple Parts which are so graduated that the terminal member is the smallest. This fact will be found of great importance in any attempt to conceive the physical process of the formation of Multiple Parts, and, pending a full discussion of this and kindred processes, it may be remarked that such a fact strikingly brings out the truth that the whole Series of Multiple Parts is bound together into one common whole, and that the addition of a member to the series may be correlated with a change in the series itself, and may occur in such a way that the general configuration of the whole series is preserved. In this case the new member of the series seems, as it were, to have been reckoned for before the division of the series into parts. This is, of course, only one way in which numerical Variation may take place; for, as was described in the previous section, additions to the series may be formed by the division of single members of the series, and in this case the configuration and proportions of the rest of the series remain normal. Examples of these two distinct methods of numerical Variation occur among Series of Multiple Parts of many kinds (digits, vertebræ, etc.).

Re-constitution of Parts of the Series

Some curious instances of what is almost a remodelling of parts of the series have been met with. Cases of this kind are known in the tessellated teeth of *Rhinoptera* (an Eagle-Ray), the most remarkable being that described and figured in *R. jussieui* by Smith Woodward in *Ann. and Mag. N. H.* ser. 6, vol. 1, 1888, p. 281. In this specimen (Fig. 5, upper diagram) the number and arrangement of the teeth were quite different on the two sides, those on the one side being normal, while those on the other were unlike any known form. This new kind of tessellation was, nevertheless, so regular and definite that had it been existing on both sides the specimen would undoubtedly have been made the type of a new species. There is, indeed, in the British Museum a unique pair of jaws in both of which a very similar tessellation occurs in a nearly symmetrical manner, and though this specimen has been described as *R. polyodon*, it is by no means unlikely that it is actually a "sport" of this kind derived from the usual formula of *Rhinoptera*.

One case in Mammals may be mentioned. This is a specimen of *Ateles marginatus* (Brit. Mus. 1214 *b*) having four premolars in each

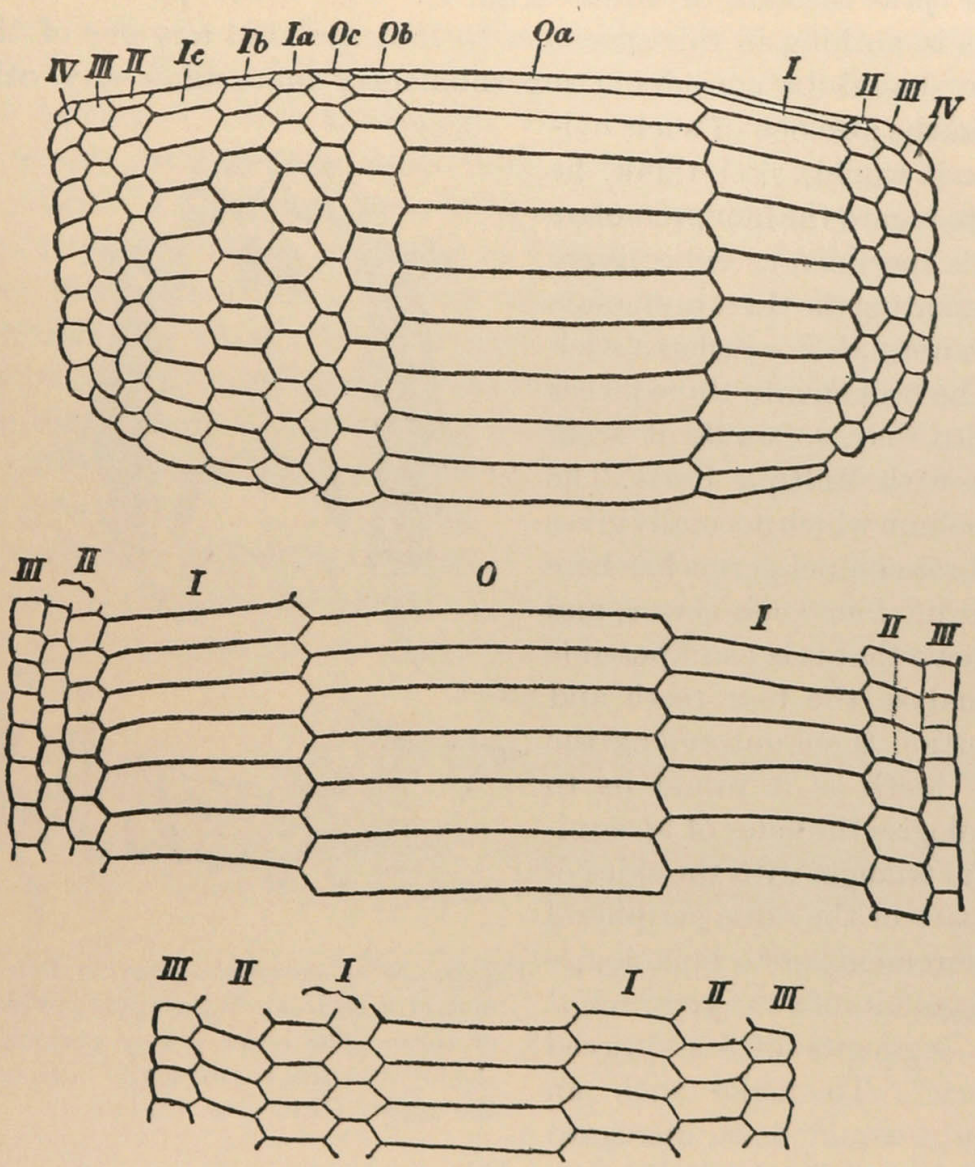


Fig. 5. *Upper diagram.* Teeth of *Rhinoptera javanica*, specimen having asymmetrical dentition (after Smith Woodward). The arrangement on the right side of the figure is normal. The lettering shows Mr Woodward's suggestion as to the correspondence of the parts.

Middle diagram. Rhinoptera sp. inc. From a Hunterian specimen in the Museum of the College of Surgeons. On the left side there are three rows of small lateral teeth, while on the right side two of these rows are represented by one row, which in places shows an indication of division.

Lower diagram. Rhinoptera javanica, in which the row of teeth marked I is on the other side represented by two rows. (After Owen, *Odontography*, Pl. xxv, fig. 2. From a specimen in Coll. Surg. Mus.)

Note.—That in these two cases, though the general proportions are maintained, the lines of division between the lateral plates on the abnormal side are not in their normal morphological positions relatively to the median plates, the interspaces on the one side corresponding to the teeth on the other.

upper jaw instead of three (Fig. 6). The lower jaw is normal. There is nothing in this specimen to indicate that any one of these teeth should be considered supernumerary more than any other; and in the absence of such evidence it would, as I think, be best to regard the four premolars in this specimen as collectively representing the three premolars of the normal. For just as a stick may be broken into three pieces or into four, so would it seem to be with Multiple Parts. The epithelium which normally gives off three enamel-germs has here given off four such germs, and I believe that it is as impossible to analyse the four teeth and apportion them out among the three teeth as it would be to homologise the sides of an equilateral triangle with the sides of a square of the same peripheral measurement, or to homologise the segments of a 4-rayed *Sarsia*[1] with segments of its 6-rayed "sport." To make such an attempt would be to disregard the plain and obvious indications of the true nature of the phenomenon, and any theory of Homology which recognises this class of problem as profitable or legitimate is, I believe, founded upon a wrong conception of the physical process of Division.

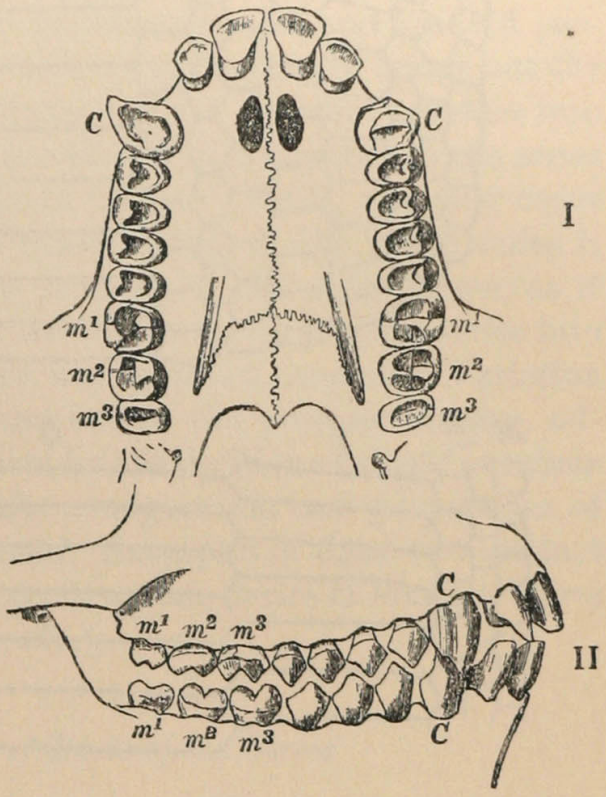


Fig. 6. *Ateles marginatus*, having four premolars on each side in the upper jaw instead of three. The lower jaw is normal, and the lower canine consequently bites behind the upper. (Brit. Mus. 1214 *b*.)

For, after all, it is with a process of physiological Division that we have here to do, and the Division which results in the formation of a series of Multiple Parts is probably a manifestation of the same physical process as the Division of a cell or the segmentation of an

[1] *Sarsia* is the Medusa of a Gymnoblastic Hydroid (*Syncoryne*). The normal form has 4 radial canals, 4 ocelli, and 4 tentacles. Three specimens having six of each of these parts are recorded, two (American) by L. Agassiz, *Mem. Amer. Acad. Sci.* IV, 248, Pl. v, fig. 5, and one (British) by Romanes, *Journ. Linn. Soc.* XII, p. 527. All of these were radially symmetrical.

ovum. Whoever will discover by what physical process an ovum segments will give us the key to the problem of the segmentation of tissues into Series of Multiple Parts; and though we are far enough from having any such knowledge, we should at least recognise that this is the problem to be dealt with, and any working hypothesis of the nature of Homology should be, at all events, in harmony with what is known of the processes of Division and should be founded upon them. Now the ordinary conception of the relationship of Homology as defined above, though it has been a useful instrument as a basis of nomenclature and so forth, is nevertheless inconsistent with the facts of Division and is founded on assumptions which are not justified, suggesting a view of the physics of Division which is wrong.

In order to appreciate this, let the reader consider, for example, the case of *Ommatophoca rossii* given above. Judged by the ordinary rules of morphological criticism, this specimen shows one or both of two things:

(1) The first premolar of *Ommatophoca may* in itself represent *two* premolars of an ancestor, or

(2) In the descendants of *Ommatophoca* the single first premolar *may* be represented by two distinct and several premolars.

One or both of these propositions may be true. If the division of the other three first premolars were as complete as that of the left p^1 there would be no indication of their origin. But if it is possible for a premolar to represent or to be represented by two premolars, without any visible indication of its double nature, may not the same be true of the premolars of other forms? May it not be true of teeth generally? And if it is true, how are the homologies of teeth to be determined? Nevertheless teeth are almost preeminently amenable to this kind of treatment. They have been studied with immense care. The facts which they present, and on which their homologies are to be determined, are remarkably compact, and of all Series of Multiple Parts they offer the best chance. But examined in the light of a knowledge of the facts of Variation, that process is found to be capable of occurring in a way which precludes the possibility of carrying out an analysis of the relation between the parts and suggests that such relationship need not necessarily exist at all. This subject cannot now be discussed further; but if any one wishes to realise the difficulties suggested by the Variations of which instances have been given, let

him read some good discussion of dental homologies, as, for example, Thomas's excellent paper[1], with these cases in his mind, and as he reads let him ask himself what margin is left for the occurrence of phenomena like this. Such schemes as that alluded to, though they have done a most useful work, and though they are ingenious, logical, and orderly, are orderly because they are made without regard to the ways of Variation, which is arbitrary and capricious and follows no order that we have yet devised.

An illustration will perhaps help to make clear the point at issue. The received view of homology supposes that a varying form is derived from the normal much as a man might make a wax model of the variety from a wax model of the type, by small additions to, and subtractions from, the several parts. This may, to our imaginations, seem, perhaps, the readiest way by which to make the varying form if we were asked to do it; but the natural process differs in one great essential from this. For in nature the body of the varying form has never *been* the body of its parent and is not formed by a plastic operation from it; but in each case the body of the offspring is made again from the beginning, just as if the wax model had gone back into the melting-pot before the new model was begun.

The present system of Homology must probably be retained as a basis of notation, imperfect though it is and though it is founded on a misconception of essential facts. It is likely that many will be disposed to doubt the reality of this misconception, and I can only ask that they should suspend judgment until the whole evidence can be produced. In the meantime this summary of facts and conclusions is put forward, together with a few "Prerogative Instances," in the hope that some one may be thereby attracted to a most powerful and fascinating method of zoological research.

[1] *Phil. Trans.* 1887, vol. CLXXVIII, B, p. 443.

SOME CASES OF VARIATION IN SECONDARY SEXUAL CHARACTERS STATISTICALLY EXAMINED

[*Proceedings of the Zoological Society*, 1892]

It is a familiar fact that many insects are provided with long, chitinous horn-like processes of various shapes and forms. Such horns are sometimes present in both sexes, but more commonly they attain their chief development in the male only. Among beetles the most striking examples are found in the Lamellicorns, many of which have horns of great size on the head, or on the thorax, or on both. Analogous developments are seen in the great mandibles of the males in some Lucanidæ, of which the stag-beetle (*Lucanus cervus*) is a common representative. In the majority of these forms the similar parts of the females are either not produced at all or are much smaller. Now in many species having these curious horns in the male sex, it has long been observed that the males are not all alike in the degree to which the horns are developed; but that, on the contrary, some of the males may bear massive horns of prodigious size, while other males of the same species have hardly any horns at all, being in fact very like females. The males with the great horns are in common parlance known as "high" males, those with the rudimentary horns being "low" males. A good series of figures illustrating the phenomenon is given by Darwin[1], and examples of such Variation in *Odontolabis* etc. are exhibited in a show-case in the Natural History Museum at South Kensington.

The phenomenon of great Variation in the development of horns present in the males as a secondary sexual character is not peculiar to beetles, though in them it perhaps reaches a climax. A similar case is presented for instance by the common earwig (*Forficula auricularia*), in which the terminal forceps are in some males no larger than those of the female, while in others they are three times the size.

The investigation we proposed to ourselves was as follows. Taking a species in which the horns of the male are sometimes small and sometimes of great size, we wished to see if individuals having any one degree of development of horns are more frequent than those having other degrees of development. The high males are an extreme form, and the low males are again an extreme form: would it then be found, on inquiry, that the mean form between these two is the commonest?

[1] *Descent of Man*, 1871, vol. I, pp. 368–375.

To those who are acquainted with the statistics set forth by Galton in *Natural Inheritance* and elsewhere, it will be well known that measurements of certain quantities, as, for example, those of the stature of Englishmen, group themselves around a mean form in such a way that the curve representing the frequency of occurrence of the several measurements has the form known as a curve of Frequency of Error. In other words, there is a mean stature for that group of persons, and variations from this mean are rarer in proportion as they depart from it. Persons of mean stature are common, while the tall and the short are rarer. This group of individuals may then be described as *monomorphic* in respect of stature. If, on the other hand, it were found that tall persons were common and short persons were common, but persons of middle height were rare, such a group might be called *dimorphic* in respect of stature, and the curve representing the frequency of their various statures would not form one Curve of Error with one peak, but would have *two* peaks. In two of the three examples about to be described, the statistics showed that such dimorphism does actually exist, and that it is not the mean form which is the commonest, but rather the moderately high and the moderately low. After these remarks we may now describe our observations.

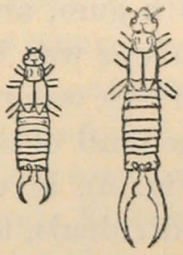
I. Forficula auricularia. (*The Common Earwig*)

In a visit to the Farne Islands off the coast of Northumberland it was noticed by one of us that these small rocks were inhabited by vast quantities of earwigs. The Farnes are a group of basaltic islands about 3–5 miles out to sea, few of them having human habitations. They are a well-known breeding-place for sea-birds of many kinds. Above high-water mark most of the rocks are covered with a deep black vegetable mould in which *Silene maritima* grows luxuriantly, constituting the chief vegetation, and it is in this that the burrows of the puffins are for the most part made.

The abundance of earwigs was most extraordinary. Under every stone or tussock there was an almost continuous sheet of earwigs. This was the case not only among the sea-birds' nests, but also round the light-keepers' houses where no birds build. It did not seem, therefore, that the excessive quantity of earwigs was necessarily connected with the presence of the nests.

It was at once seen that amongst these earwigs were many males with extremely long forceps, like that shown in Fig. 1, II. The usual

form is seen in Fig. 1, I, both figures being natural size. We shall refer to these two forms as "high" and "low" males respectively.



I. II.

Fig. 1. *Forficula auricularia*, the common earwig. I. Low male. II. High male.

It appears that the high male is known from many places in England and elsewhere, and that it was made into a distinct species by Stephens[1] under the name *F. forcipata*. This species has not been retained by later authorities (see Fischer[2] and Brunner von Wattenwyl[3]). After the visit to the Farnes, the high males were found on the mainland near Bamborough in fair quantity, though not so abundant as on the Farnes. We have received also a large sample of earwigs collected in a Cambridge garden, containing 163 males, of which 5 would come into the "high" class. A sample kindly collected for us by Dr Norman, F.R.S., in his garden at Burnmoor, near Durham, contains no high male. The great abundance of high males at the Farnes seems to be quite exceptional.

With a view to determining the frequency of the high and low forms, 1000 of these earwigs were collected for us by Miss A. Bateson on Sept. 12, 1892. The whole were taken in one day from three very small islands known as the Knocksies and Widerpern, which are joined to each other at low tide.

Of the 1000 specimens 583 proved to be mature males. Before giving the results of the measurements, it is perhaps necessary to give the reasons upon which we believe these specimens to have been all adult. In this matter we rely partly on the judgment of Dr Sharp, F.R.S., who has most kindly assisted us in many ways throughout this investigation, and was so good as to take part in the work of measurement. We are informed by Dr Sharp that the full development of the elytra is only reached in the adult state in *F. auricularia*, and we have been careful to include no specimen having imperfect elytra. As may be seen in the figures, the development of the elytra in the high and low males is the same. Besides this, it is to be remembered that in most localities the high male is either unknown or very scarce, and it cannot be doubted that in these places the low males are really mature. Lastly, we know by the analogous case of horned beetles that high males coexist with low males, both being in this case of course mature. We think, therefore, that we are justified in considering that the 583 males available for measurement were all adult.

[1] *British Entomology*, 1835, VI, p. 6, Pl. XXVIII, fig. 4.

[2] *Orthoptera Europœa*, 1853, p. 74. [3] *Prodr. d. europ. Orthop.* 1882, p. 12.

These specimens were laid out on squared millimetre paper covered with gum, and while the gum was still wet the posterior end of the forceps was brought up to one of the lines, and the length of the forceps was read to the nearest half millimetre, which is well within the limit of error. The results are set out in the accompanying curve (Fig. 2), in which the figures on the ordinates denote numbers of individuals, those on the abscissæ denoting millimetres. The smallest

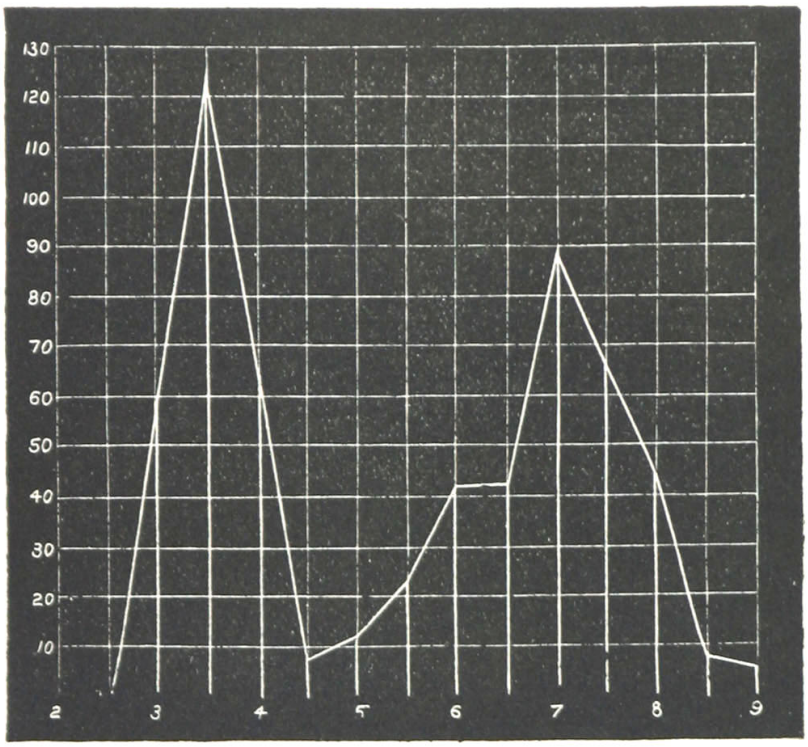


Fig. 2. Curve showing frequency of occurrence of forceps of various lengths in male earwigs (*F. auricularia*). Ordinates give numbers of individuals; abscissæ give length of forceps in mm.

length of forceps was 2·5 mm., and the greatest 9 mm. As the curve shows, the greatest frequency is grouped about 3·5 mm. and 7 mm. respectively. The mean form, having forceps of moderate length, 4–6 mm., is comparatively rare. We consider that the number of cases is enough to justify the acceptance of these statistics, and it is unlikely that a greater number of cases would much alter the shape of the curve[1]. The size of the forceps in the females scarcely varies at all, probably less than 1 mm. in the whole sample.

[1] In most insects having high and low males, the high males are large in every way, while the low males are small. That this is so, generally speaking, in these earwigs was clear, but it is not possible to get reliable measurements of total length, owing to the fact that the abnormal segments "telescope" into each other. Hence no examination of the correlation between total length and the length of the forceps could be attempted. There is nevertheless no doubt that the ratio of the length of the forceps to the total length is higher in high males than in the low.

It is perhaps unnecessary to say that this result is of considerable importance to an appreciation of the way in which Variation may occur. There is here a group of individuals living in close communion with each other, high and low, under the same stones. No external circumstance can be seen to divide them, and yet they are found to consist of two well-marked groups, containing about equal numbers. To those who are acquainted with the chapter on Organic Stability in Galton's *Natural Inheritance*, this will be recognised as an instance of Variation about two positions of stability, the intermediate position being one of less stability. In the common language of naturalists, the facts of this case suggest that there is, for some wholly unknown reason, a dimorphism among the males of these earwigs, maintained though all live together. In cases of dimorphism some have thought fit to speculate on the possible utility of the phenomenon. We know no basis of fact from which these discussions may be properly attempted, and we leave these matters to those who are satisfied with such methods of biological inquiry and have leisure and ingenuity to pursue them.

For the present we are content to recognise that in this case of the earwig there is evidence of a definite and partially discontinuous Variation in respect of a secondary sexual character.

II. Xylotrupes gideon

We are indebted to Baron A. von Hügel for a large supply of this species. They were collected by him at a height of 4000–5000 feet in the Willis Mountains, Kediri, Java, in February to April, 1878. In Fig. 3 (p. 198) the males of this species are represented. As there seen, in this sex two horns are present, the one produced from the head, the other from the thorax. The two horns lie in the same vertical plane, and each ends in a small fork. Taken together, these two horns thus constitute a pair of forceps, which can be opened by depressing the head. The points of the forceps do not exactly meet, but the point of the cephalic horn in high males is overlapped by that of the thoracic horn. As the figures show, there is very great variation in the degree to which these horns are developed in the male, the three drawings representing "high," "medium," and "low" males respectively. In the female neither horn is developed, but there is considerable variation in total length. As may also be seen in the figures, those males which have very large horns are also in other ways large individuals, while the males with small horns are small individuals. But though there is some correlation between absolute size

and the degree to which the horns are developed, our measurements have shown that this correlation is not perfect. It is of course clear that the ratio of length of the horns to that of the body is greater in the high males than in the low.

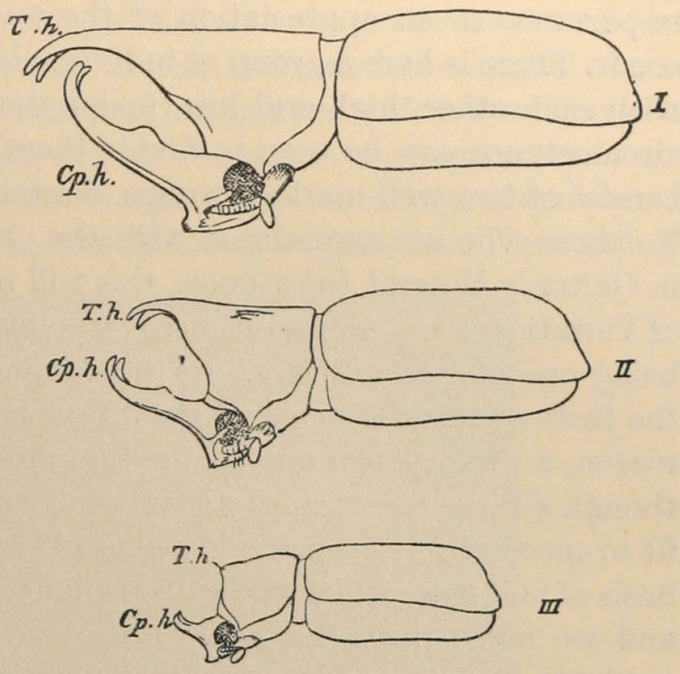


Fig. 3. Diagrams of *Xylotrupes gideon*, ♂, seen from side. Legs not shown. I, High male. II, Medium male. III, Low male. *T.h.*, thoracic horn; *Cp.h.*, cephalic horn.

Baron von Hügel gave us some interesting particulars as to the natural history of these beetles. They were collected in the height of the breeding season, perhaps the greater number being found coupled. It was noticed that large males were often attached to small females and the reverse, but there appeared to be no regularity in this. In view of the circumstance that there are scarcely any observations as to the functions of the horns of beetles, the following statements of Baron von Hügel are especially noteworthy. He says that the animals were caught by himself and by natives, and were tied up with pieces of bast. When they were brought home and untied, the males immediately sought out the females, and seizing them transversely, carried them about, held between the two horns, with evident satisfaction. He tells us that this was observed again and again, and was clearly a definite habit. The males with small horns, though unable to lift the females, nevertheless made ludicrous efforts to do so. In answer to the question whether it was observed that these small males did not succeed in obtaining females in the state of nature, Baron von Hügel tells us that he has no reliable recollection on this point.

The habit described above is not confined to *X. gideon*, for Baron von Hügel observed it also on one occasion in the case of *Chalcosoma atlas*, the well-known atlas-beetle. A pair of this species from Java were presented by him to the Cambridge Museum, which were thus found, the female being carried between the horns of the male. In view, therefore, of the fact that the horns of many species are in various ways disposed as a pair of forceps, it is possible that this may be a habit widely spread; but that such a function cannot be attri-

buted to all the cases of horns is shown by the fact that in many species the horns do not form a pair of forceps.

In 342 males of this beetle the cephalic horn was measured with compasses from the angle of the terminal fork to the edge of the ridge into which the horn is proximally and ventrally reflected, just in front of the eyes. The results obtained are tabulated in Fig. 4, according to the common system. Each dot represents a case, and the ordinates thus give the numbers of cases, while the abscissæ show the lengths of the horns; for clearness these measurements are shown four times

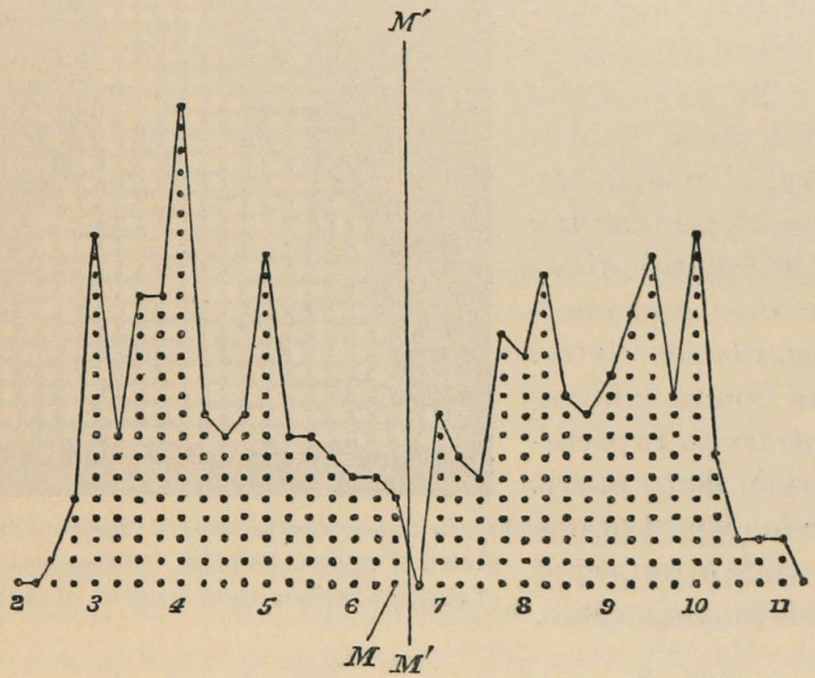


Fig. 4. Diagram showing frequency of various lengths of the cephalic horns in *Xylotrupes gideon*, ♂. *M*, mean case; *M'*, mean value. Ordinates show number of cases; abscissæ show lengths four times nat. size. The numbers give the lengths in lines.

the natural size. The shortest cephalic horn was 0·4 cm., while the longest was 2·4 cm. As the diagram shows, in the neighbourhood of the mean value (*M'*) for the length of horn the specimens were few, while the moderately high and moderately low males are common, the two groups being about equally numerous.

Measurements of the thoracic horn showed a similar dimorphism; but, for the reason that it is not possible to measure this horn apart from the thorax, these measurements are not so satisfactory.

The length of the elytra was also measured, and it may perhaps be taken as a measure of the body-length. For various reasons it is hard to obtain any more satisfactory measurement of the body-length. Such a measurement must either include the variable horns or else must depend on the degree of flexion of head or thorax

The result of the measurement of the elytra is perhaps unexpected in view of the knowledge that there is dimorphism in respect of the cephalic horn. Fig. 5 shows the result of grouping the statistics as to the frequency of the various lengths of elytra, and it is hence clear that the mean form is the commonest, just as it is in the case of the stature of a given human community. Though dimorphic in respect of the length of the horns, these males are thus monomorphic as regards the elytra. There is of course nothing really contrary to expectation in the fact that a race is dimorphic in respect of one character while in respect of another it is monomorphic.

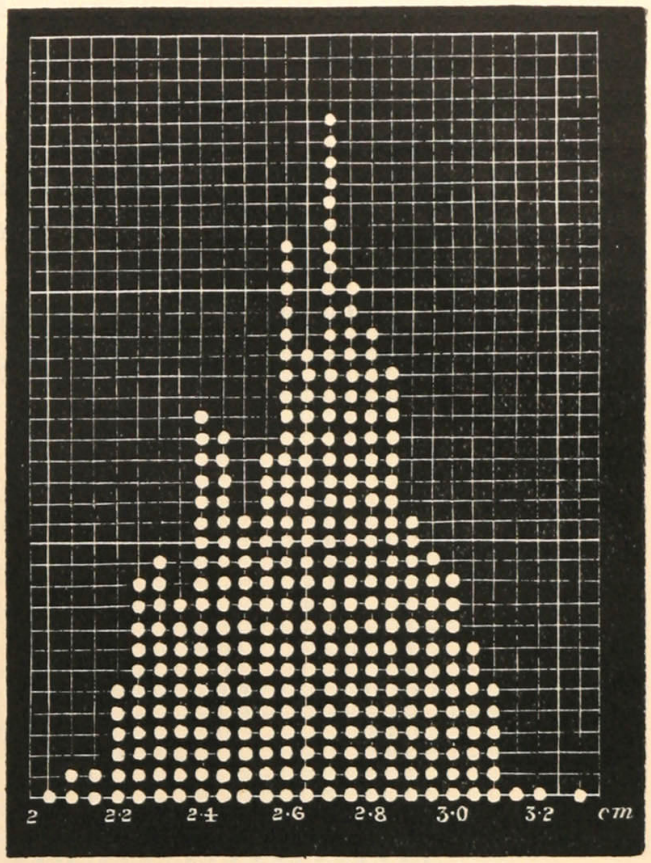


Fig. 5. *Xylotrupes gideon*, ♂. Table of frequency of elytra of various lengths. Ordinates show number of cases; abscissæ show lengths of elytra in cm.

III. Lucanus cervus. (*The Stag-beetle*)

Of this insect we have no quantity of males sufficient to justify a statement that in respect of the development of the mandibles it is monomorphic or dimorphic. It is well known that very striking differences are found between high and low males in this species.

Males to the number of 115 obtained at Woking in 1891 and 1892 have been measured. The lengths of the mandibles from the apex to the internal angle between the base and the head were taken with compasses, and the result is exhibited in Fig. 6. The fact that this sample is monomorphic is quite clear, for the numbers are plainly grouped round the middlemost value. But in this case there is serious reason to doubt whether the sample examined contains really low males. In our experience of the earwig's forceps and the *Xylotrupes* horns, the low males are almost like the females; but in the case of the stag-beetle the mandible of the lowest male seen was much greater than that of the females. It seems possible that in the stag-beetle

the truly low male is either very rare or does not occur, and that the existing individuals belong to a group answering to those which were found in *Xylotrupes* above the middlemost value. There is in fact a possibility that we have in the stag-beetle a case which is the converse of that of the earwig. In most places the low male earwig is to be found, the high male being absent or very scarce, but in the stag-beetle it is the high male that is common while in most places the low male is absent or scarce.

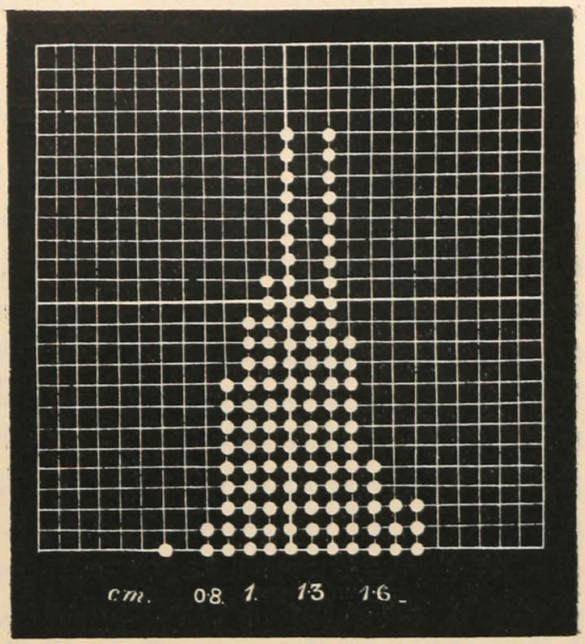


Fig. 6. Table of frequency of various lengths of mandible in *Lucanus cervus*, ♂. Ordinates show number of cases; abscissæ give lengths of mandibles in cm.

In this case, and in that of *X. gideon* also, the ratio of the mandibles or horns to the total length is higher in the high males than in the low males; or, in other words, though the body of a high male is larger than that of a low male, the horns of the high male are still larger in proportion to the body than those of the low male.

In conclusion we would call attention to the fact that fantastic secondary sexual horns present one of the most difficult problems in Evolution, for as to their modes of origin even guesses can scarcely be made. To their production a considerable expenditure of energy is clearly needed, and yet in many cases they have no obvious function. They are, further, notoriously variable. Darwin on the whole was disposed to regard them as ornaments. The knowledge therefore that Variation in the degree of development of these structures may be discontinuous is of material assistance to the formation of any conception as to the manner of their origin. The question may be asked, does the dimorphism of which cases have now been given represent the beginning of a division into two species, or rather a division which might be accentuated so as to lead to such division? To this question we have no answer to make, but such a possibility may well be remembered.

We must express our thanks to Messrs Macmillan for their kindness in allowing us to use the drawings of Figs. 1–4, which have been prepared by them in illustration of a forthcoming book by one of us on the subject of Variation.

THE ALLEGED "AGGRESSIVE MIMICRY" OF *VOLUCELLÆ*

[*Nature*, XLVI, 1892]

IN the course of a review (*Nature*, Oct. 6, 1892, p. 535) of a book, *Animal Coloration*, by Mr Beddard, Mr Poulton takes occasion to refer to a theory professing to elucidate the resemblance of *Volucellæ* to humble-bees, etc. This reference is occasioned by the suggestion of a counter-hypothesis by Mr Beddard. The view adopted by Mr Poulton[1] is that proposed by Kirby and Spence, and subsequently alluded to by Künckel d'Herculais[2] and others; but as Mr Poulton makes no reference to these authorities he may be assumed to accept the full responsibility. In the place named he says: "The boldness of these enemies sometimes depends on the perfection of their disguise. Thus the larvæ of flies of the genus *Volucella* live upon the larvæ of bees and wasps. *Volucella bombylans* occurs in two varieties, which prey upon the humble-bees *Bombus muscorum* and *B. lapidarius*, and are respectively like these Hymenoptera. The resemblance is very perfect, and the flies enter the nests to lay their eggs." Mr Beddard[3] criticises the view that the fly resembles the bee that it may with impunity enter the nest, and proposes to look on the presence of the fly's larvæ in the bees' nests as akin to the presence of supposed "pets" in the nests of ants. As Poulton points out, this suggestion leaves the original difficulty of the likeness of the fly to the bee untouched.

Having little interest in either of these speculations, which seem fantastic and premature, it is with reluctance that I take part in the discussion. The case, however, of *V. bombylans* is not only interesting as a striking, and to us in England a most accessible instance of the phenomenon of Mimicry, but as an example of Variation it is almost unique among animals, while among plants perhaps it is paralleled only by Darwin's famous case of the peach and the nectarine. It is besides a case well suited for experiment and close observation. The nests of surface-building bees may towards evening be lifted bodily, bees, *Volucellæ*, and all, with a spit of earth, and transferred to a box. This may be taken home and set next morning on a window-sill, when on opening the box the bees will go on with their work for the

[1] *Colours of Animals*, 1890, p. 267.

[2] *Organ. et Dével. des Volucelles*, Paris, 1875.

[3] *l.c.* p. 225.

rest of the summer. If any one seeks an opportunity of honestly trying to get to the bottom of a case of Mimicry, instead of speculating about it at large, he can scarcely find a better case than this. The need for such observations is great, for the account confidently given by Poulton, though according well with his hypotheses, accords with the truth less well.

In these circumstances it may not be out of place to give a brief statement of the facts as they were established by entomologists long ago. The *Volucellæ* are a small group of flies, containing four British species[1]; of these most if not all resemble various Hymenoptera. The commonest and most remarkable is *V. bombylans*, which may be seen in any English hedgerow on a sunny day in early summer. This fly exhibits the rare condition of existing in two distinct forms in both sexes. The one form is black with a red tail, in no small degree resembling a small worker of a red-tailed humble-bee, such as *B. lapidarius* L. or *B. Derhamellus* Kirb. The other form has a yellow border to the thorax, yellow hairs on the antero-lateral parts of the abdomen, and a grey tail, to an equal degree resembling a small worker of one of the several yellow-banded humble-bees, *e.g. B. hortorum* L., *B. terrestris* L., or *B. Scrimshiranus* Kirb. Both varieties occur in both sexes and are about equally common. The problem of the evolution of these distinct forms is thus one of the most complex. Some may ask, If the varieties are thus distinct, how are they known to be one species? The evidence of this is (1) that no point of structure can be found to differentiate them, (2) that males of the one variety have been seen coupled with females of the other and *vice versa*[2], and lastly (3) that intermediate forms have been found as rarities[3]. This evidence may not satisfy all, but as regards Mr Poulton the identity of the two as one species is not in dispute, for he admits this.

But though the likeness of *V. bombylans* L. and its var. *mystacea* L. (= *plumata* de Geer) to the red-tailed humble-bees and to the yellow-banded humble-bees respectively is really close, neither these forms nor the less common var. *hæmorrhoidalis* Zt. present any special likeness to *B. muscorum* L., which has a bright brown thorax and a grey abdomen. It is true that Künckel has spoken of a resemblance between the var. *mystacea* and *B. muscorum*, but it is hard to see upon what ground, for indeed it is much as if one were to liken a tabby cat

[1] Verrall, *Cat. Brit. Dipt.* 1888.

[2] Macquart, *Suites à Buff.* p. 479; Zeller, *Stet. ent. Ztg.* 1842, p. 66.

[3] Erichson, *Stet. ent. Ztg.* 1842, p. 115.

to a fox. As Künckel himself says, the great resemblance of the fly is to the yellow-banded *B. hortorum*.

To return to Mr Poulton's statement, he says that the two varieties prey upon "*Bombus muscorum* and *B. lapidarius*, and are respectively like these Hymenoptera." These words contain an ambiguity which I cannot believe intentional. But supposing for a moment that one of the varieties *were* like *B. muscorum* (which it is not), the sentence must be taken to mean that each variety preys upon the species of bee which it most resembles, the red-tailed variety on the red-tailed bee and the yellow variety on the other. This is indeed demanded by the hypothesis of "Aggressive Mimicry." In this form the statement is often made, though I never met it elsewhere in print. I invite Mr Poulton to produce observations in support of that statement. If he will establish it he will do a useful work. When this statement was written I must believe that Mr Poulton had not read the several authorities on the subject, many of whom relate how both varieties have been reared from the nests of each type of bee, both from the red-tailed and from the yellow-banded[1]. It is still possible that both varieties are born of one mother, and it is possible, too, that each female does her best to choose the nests of a bee like herself, but in support of this hypothesis I know no evidence; and indeed Künckel[2], after considering this possibility, gives it as his opinion that probably the varieties of *V. bombylans* lay indifferently in the nests of all *Bombi*. From the omission of these facts, which to an appreciation of the evidence are vital, we should infer that Mr Poulton was not acquainted with Künckel's work, were it not that he repeats Künckel's selection of *B. muscorum* as a form resembled by one of the two varieties.

But though Mr Poulton is wrong in saying that either variety specially resembles *B. muscorum*, he is right in saying that *V. bombylans* preys on this bee's nests, for *both* varieties have been bred from them, even from the same nest[3]. In my rooms at this moment are several nests of *B. muscorum*, each containing many larvæ of *V. bombylans*, resting for the winter, to emerge in summer, as I hope.

There is then evidence that the two varieties, though they may breed together, yet remain substantially distinct; and that though they respectively resemble different species of bees, they are both found together, not only in nests of bees which they resemble, but

[1] Künckel, p. 58; Drewsen, *Stet. ent. Ztg.* 1847, p. 211; F. Boie, Kröyer's *Naturh. Tids.* 1838, p. 237.

[2] P. 58.

[3] *Ibid.*

also, and in my own experience more abundantly, in the nests of another bee which they do not resemble.

Mr Poulton further omits to mention that *V. pellucens*, though in nowise resembling the common wasp, yet lives in its nests, together with *V. inanis* which does resemble a wasp, and *V. zonaria* which is like a hornet[1]. This fact also I commend to Mr Poulton's ingenuity.

The publication of statements like this of Mr Poulton's, omitting most salient facts—facts, besides, which, though adverse to his speculations, add a ten-fold interest to the subject—is surely unfortunate. It may be replied that Mr Poulton's book is of a popular character and does not aim at the completeness of scientific work; but in making choice of evidence, even for popular exposition, it is well to remember that the value of facts is not to be measured by the ease with which they may be momentarily fitted to the sustenance of a facile hypothesis.

[1] Künckel, pp. 54 and 55

THE ALLEGED "AGGRESSIVE MIMICRY" OF *VOLUCELLÆ*

[*Nature*, XLVII, 1892]

MR POULTON'S letter[1] calls for few words in reply. I invited Mr Poulton to produce observations in support of his statement that the two varieties of *Volucella bombylans* lay in the nests of the bees which they respectively resemble. To this invitation Mr Poulton has not responded. He tells us that his account represented "a very general impression"; that the same impression has been set forth in a showcase at the Museum of the Royal College of Surgeons; that even if he were mistaken it was well, if through his mistake the truth shall the more abound. It is thus admitted that in making that statement Mr Poulton relied not on original authorities, but on the general impressions of others. That these impressions are in any sense correct there is as yet no evidence to show.

Compared with this, Mr Poulton's error as to *Bombus muscorum* is of course comparatively trifling, and it would be useless to pursue the matter were it not for discoveries made in the process of unravelling it.

I pointed out that *V. bombylans* is common in nests of *B. muscorum*, a bee which it does not resemble. Mr Poulton in reply maintains the opinion that *V. bombylans* var. *mystacea* does resemble *B. muscorum*. In defence of this statement he refers to (1) the showcase at the Royal College of Surgeons, where the resemblance is set forth; (2) a recent book, *Animal Intelligence*, by Mr Lloyd Morgan, where the resemblance is again asserted and illustrated by figures of insects in the similar showcase at the Natural History Museum.

In following up these clues I came to unexpected results. (1) There is at the College of Surgeons a showcase, as stated, illustrating the likeness of *Volucellæ* to humble-bees. The label states that "the resemblance enables them [the flies] to escape detection." Two bees are exhibited bearing a good likeness to the var. *mystacea*, and, as Mr Poulton says, they are labelled "*B. muscorum*." The one, however, is a worker of *B. sylvarum* L., and the other is probably a male of the same species. Neither can be mistaken for *B. muscorum*, which they do not resemble.

(2) At the Natural History Museum bees of several species are shown besides the *Volucellæ*, with a similar statement that the

[1] [See *Nature*, XLVII, Nov. 10, 1892, p. 28. ED.]

resemblance enables the flies "to enter the nest of the bee without molestation." Not one of these bees is *B. muscorum*, nor are any of them said to belong to this species, for no names are given. Nevertheless, on turning to Mr Lloyd Morgan's book, which I had not before seen, I find the statement (p. 90) that *V. bombylans* "closely resembles" *B. muscorum*, the passage continuing in the words of the Natural History Museum label. Figures are added showing the two forms of *V. bombylans* and two very different bees, *both* marked "*B. muscorum*." Now the figures are from *photographs* of certain specimens in the showcase, and on reference to the specimens in question, it appears that one of them is a yellow-banded humble-bee (perhaps *B. hortorum*), while the other is one of the red-tailed humble-bees! These two are put out to match *V. bombylans* and the var. *mystacea* respectively, and of course have no likeness either to each other or to *B. muscorum*, though both are referred to this species by Mr Lloyd Morgan.

Mr Poulton's choice of *B. muscorum* as a form resembled by the var. *mystacea* probably therefore arose from the wrong naming at the Royal College of Surgeons. How Mr Lloyd Morgan came to call the two different bees by the name *B. muscorum*, which belongs to neither, I cannot tell. Perhaps this is in part an echo of Mr Poulton's previous mistake.

Any one by reference to a collection of bees may easily satisfy himself that the common and ordinary *B. muscorum*, with its bright brown thorax, does not resemble *V. bombylans*, though this fly is common in its nests, just as *V. pellucens* lives in wasps' nests, though it does not resemble a wasp.

In the absence of direct evidence in its favour, and inasmuch as it is inconsistent with many ascertained facts which were specified in my first letter, the hypothesis of "Aggressive Mimicry" should surely be withdrawn.

No speculation is needed to enhance the exceptionally interesting facts of the Variation and the resemblances of the *Volucellæ*. If a number of people will set to work on this problem in the way suggested, there is, I think, a fair chance of considerable results. It was in the hope that such effort may be made that I drew attention to the matter, and I am really sorry that Mr Poulton should be hurt thereby. Nevertheless, I cannot but regard his account of the matter as an example of the way in which statements pass on from one writer to another, but prove on inquiry to be baseless.

AN ABNORMAL FOOT OF A CALF

[*Proceedings of the Zoological Society*, 1893]

Mr W. Bateson exhibited an abnormal foot of a calf, which had been forwarded to him for examination by the kindness of Mr W. L. Sclater.

The specimen was a right fore-foot, bearing three digits disposed almost symmetrically with regard to the axis of the limb. Of the carpus only the distal row remained, consisting of the usual two elements, a trapezoido-magnum and an unciform. External to the unciform the small rudiment, considered as representing the fifth digit, was of the usual size and proportions. The upper end of the metacarpal bone presented no peculiarity. Peripherally, however, instead of the usual two articular surfaces the metacarpal in this limb had *three* articular surfaces, all standing in the same plane as those of a normal limb. Each articular surface is well formed and has a large trochlear ridge. The central articular surface differs a little from the other two, being slightly crowded against the external one. In it also the trochlear ridge does not exactly divide the articular surface, but is rather nearer to the external side. With each of the three surfaces articulates a digit containing three phalanges of full length. Over each articulation is a pair of normal sesamoids, three pairs in all, instead of two pairs.

Each digit bears a hoof. The hoof of the middle digit is *convex* on both sides, but each of the lateral hoofs is convex on its outer side and concave on the side turned towards the hoof of the middle digit. The small accessory hoofs, the *ergots* of French writers, are normal and stand in their usual positions with regard to the limb, one being above and slightly external to the metacarpo-phalangeal articulation of each of the outer digits. The limb is almost exactly symmetrical about a line taken through the centre of the middle toe. Each of the toes had well-formed flexor and extensor tendons.

In the normal metacarpus of the ox there is in the peripheral third a median groove of some depth, indicating the line of demarcation between metacarpals III and IV. It is in this groove that the foramen for the nutrient artery is placed on the posterior surface of the limb. In the abnormal specimen there is no median groove, but on either side of the middle digit there is such a groove, indicating the lines of

demarcation between the parts of the metacarpus belonging to each of the three digits. The groove between the middle and external digit is very slightly the deeper of the two, and in it is placed the foramen for the nutrient artery on the posterior surface.

The specimen was an old one and no particulars as to parentage or to the condition of the other limbs were to be had. It was mentioned that this case differed from that of the three-toed Cow described by Neville Goodman, *Journ. Anat. and Phys.* 1868, in that there was in the present example an almost perfect symmetry about the middle axis of the foot.

THE COMMON PILCHARD

[*Proceedings of the Zoological Society*, 1894]

Mr W. Bateson exhibited six specimens of the common pilchard (*Clupea pilchardus*) showing Variation in the number and size of the scales. The specimens had been received from Mr Matthias Dunn, of Mevagissey, Cornwall. In each of them the scales over a greater or less area of the body were smaller and more numerous than in the normal fish. Similar specimens were exhibited to the Society by Mr Bateson in 1890 and had been described in the *Proceedings*[1] as examples of abnormal repetition of parts. In that paper reference was made to an account of a similar specimen that had been given by the late Mr F. Day[2], who took a different view, being of opinion that the fish was a hybrid between the pilchard and the herring. For reasons then given it was urged that the evidence of hybridity was unsound, and it was represented that the abnormality was more probably due to Variation.

The new cases fully bore out the view then taken. Except in the matter of the scales, each of the six examples was in all respects a true pilchard, having the normal sculpture on the opercula, the high number of gill-rakers characteristic of the pilchard, and the histological features normally found in the scales of the pilchard. In the matter of the gill-rakers the lowest number seen in the abnormal fishes was 70 and the highest 89, most of them having about 78. The numbers seen in normal herrings are considerably lower than these.

In four of the new specimens the small abnormal scales extended over the posterior half of one side only. In one specimen both sides were almost uniformly covered with the small scales. In the sixth specimen the posterior half of one side showed the small scales, and on the other side there was in about the middle of its length a circular patch of very small scales, the remainder of the scaling being normal or nearly so. Unfortunately the specimens had been somewhat rubbed and the precise numbers of the scales cannot confidently be given. Speaking in general terms, it may be said that in the areas of abnormal scaling the size of the scales was about half that of the normal scales. All the specimens were well grown and in good condition, ranging from 7 to $8\frac{1}{2}$ inches in length.

[1] *Proc. Zool. Soc.* 1890, p. 586 [p. 121 *supra*. Ed.]. [2] *Op. cit.* 1887, p. 129, Pl. xv.

MATERIALS FOR THE STUDY OF VARIATION

[Macmillan and Co., London, 1894]

PREFACE

THIS book is offered as a contribution to the study of the problem of Species. The reasons that have led to its production are as follows.

Some years ago it was my fortune to be engaged in an investigation of the anatomy and development of *Balanoglossus*. At the close of that investigation it became necessary to analyse the meaning of the facts obtained, and especially to show their bearing upon those questions of relationship and descent which modern morphology has attempted to answer. To this task I set myself as I best might, using the common methods of morphological argument and interpretation, and working all the facts into a scheme which should be as consistent as I could make it.

But the value of this and of all such schemes, by which each form is duly ushered to its place, rests wholly on the hypothesis that the methods of argument are sound. Over it all hung the suspicion that they were not sound. This suspicion seemed at that time so strong that in preface to what I had to say I felt obliged to refer to it, and to state explicitly that the analysis was undertaken in pursuance of the current methods of morphological criticism, and without prejudging the question of possible or even probable error in those methods.

Any one who has had to do such work must have felt the same thing. In these discussions we are continually stopped by such phrases as, "if such and such a Variation then took place and was favourable," or, "we may easily suppose circumstances in which such and such a Variation if it occurred might be beneficial," and the like. The whole argument is based on such assumptions as these—assumptions which, were they found in the arguments of Paley or of Butler, we could not too scornfully ridicule. "If," say we with much circumlocution, "the course of Nature followed the lines we have suggested, then, in short, it did." That is the sum of our argument.

Were we all agreed in our assumptions and as to the canons of interpretation, there might be some excuse, but we are not agreed. Out of the same facts of anatomy and development men of equal ability and repute have brought the most opposite conclusions. To take for instance the question of the ancestry of Chordata, the problem on which I was myself engaged, even if we neglect fanciful suggestions, there remain two wholly incompatible views as to the lines of Vertebrate descent, each well supported and upheld by many. From the same facts opposite conclusions are drawn. Facts of the same kind will take us no further. The issue turns not on the facts but on the assumptions. Surely we can do better than this. Need we waste more effort in these vain and sophistical disputes?

If facts of the old kind will not help, let us seek facts of a new kind. That the time has come for some new departure most naturalists are now I believe beginning to recognise. For the reasons set forth in the Introduction I suggest that for this new start the Study of Variation offers the best chance. If we had before us the facts of Variation there would be a body of evidence to which in these matters of doubt we could appeal. We should no longer say "*if* Variation take place in such a way," or "*if* such a Variation were possible"; we should on the contrary be able to say "since Variation *does*, or at least *may* take place in such a way," "since such and such a Variation *is* possible," and we should be expected to quote a case or cases of such occurrence as an observed fact.

To collect and codify the facts of Variation is, I submit, the first duty of the naturalist. This work should be undertaken if only to rid our science of that excessive burden of contradictory assumptions by which it is now oppressed. Whatever be our views of Descent, Variation is the common basis of them all. As the first step towards the systematic study of Variation we need a compact catalogue of the known facts, a list which shall contain as far as possible all cases of Variation observed. To carry out such a project in any completeness may be impossible; but were the plan to find favour, there is I think no reason why in time a considerable approach to completeness should not be made.

Difficulty has hitherto arisen from the fact that Variation is not studied for its own sake. Each observer has some other object in view, and we are fortunate if he is good enough to mention in passing the Variations he has happened to see in following his own ends.

From the nature of the case these observations must at first be sporadic, and, as each standing alone seems to have little value, in the end they are unheeded and lost. If there were any central collection of facts to which such observations might from time to time be added, and thus brought into relation with cognate observations, their value would at once appear and be preserved. To make a nucleus for such a collection is the object of the present work.

The subject treated in this first instalment has been chosen for the reasons given in the text. Reference to facts that could not be included in this section of the evidence has as far as possible been avoided, but occasionally such reference was necessary, especially in the Introduction.

It was my original purpose to have published the facts without comment. This course would have been the most logical and the safest, but with hesitation it was decided to add something of the nature of analysis. I do this chiefly for two reasons. First, in starting a method one is almost compelled to show the way in which it is to be applied. If it is hoped that others may interest themselves in the facts, it is necessary to show how and why their interest is asked. In the old time the facts of Nature were beautiful in themselves and needed not the rouge of speculation to quicken their charm, but that was long ago, before Modern Science was born.

Besides this, to avoid the taint of theory in morphology is impossible, however much it may be wished. The whole science is riddled with theory. Not a specimen can be described without the use of a terminology coloured by theory, implying the acceptance of some one or other theory of homologies. If only to avoid misconception matters of theory must be spoken of.

It seemed at first also that the meaning of the facts was so clear that all would read it alike; but from opportunities that have occurred for the discussion of these matters I have found that it is not so, and reluctantly I have therefore made such comments as may serve to bring out the chief significance of the phenomena, pointing out what they show and what they do not show, having regard always to deficiencies in the evidence.

That this is a dangerous course I am aware. But in any discussion of a problem in the light of insufficient knowledge the real danger is not that a particular conclusion may be wrong, for that is a transient fault, but rather that the facts themselves may be so distorted as to be valueless to others when the conclusions that they were used to

show have been discarded. This danger I have sought indifferently to avoid by printing the facts as far as possible apart from all comment, knowing well how temporary the worth of these comments is likely to be. I have thus tried to avoid general statements and have kept the descriptions to particular cases, unless the number of similar cases is great and an inclusive description is enough.

Each separate paragraph relating a fact has been as far as possible isolated and made to stand alone; so that if any one may hereafter care to go on with the work he will be able to cut out the discarded comments and rearrange the facts in any order preferred, inserting new facts as they come to hand. Most of these facts are numbered for reference. The numbers are distributed on no strict system, but are put in where likely to be useful.

For almost every fact stated or mentioned one reference at least is given. When this is not the case the fact is either notorious, or else the result of my own observation. In collecting evidence I have freely used the collections of former writers, especially those of Geoffroy St Hilaire, Ahlfeld, and Wenzel Gruber, but unless the contrary is stated, each passage referred to has been seen in its original place. By this system I hope I have avoided evidence corrupted by repetition. Several well-known conceptions, notably that of the presence of order in abnormality, first formulated by Isidore Geoffroy St Hilaire, have been developed and exhibited in their relation to recent views.

The professed morphologist will note that many of the statements are made on authority unfamiliar to him. I have spared no pains to verify the facts wherever possible, and no case has been admitted without remark if there was reason to doubt its authenticity. So long as skilled zoologists continue to neglect all forms that are abnormal the student of Variation must turn to other sources.

This neglect of the Study of Variation may be attributed in great measure to the unfortunate circumstance that Natural History has come to be used as a vehicle for elementary education, a purpose to which it is unsuited. From the conditions of the case when very large classes are brought together it becomes necessary that the instruction should be organised, scheduled, and reduced to diagram and system. Facts are valued in proportion as they lend themselves to such orderly treatment; on the rest small store is set. By this method the pupil learns to think our schemes of Nature sufficient, turning for inspiration to books, and supposing that by following his

primer he may master it all. In a specimen he sees what he has been told to see and no more, rarely learning the habit of spontaneous observation, the one lesson that the study of Natural History is best fitted to teach.

Such a system reacts on the teacher. In time he comes to forget that the caricature of Nature shown to his pupils is like no real thing. The perspective and atmosphere that belong to live nature confuse him no more. Two cases may be given in illustration. Few animals are dissected more often than the crayfish and the cockroach. Each of these frequently presents a striking departure from the normal (see Nos. 83 and 625) in external characters, but these Variations have been long unheeded by pupil and by teacher; for though Desmarest and Brisout published the facts so long ago as 1848, their observations failed to get that *visa* of the text-books without which no fact can travel far.

It is especially strange that while few take much heed of the modes of Variation or of the visible facts of Descent, every one is interested in the *causes* of Variation and the nature of "Heredity," a subject of extreme and peculiar difficulty. In the absence of special knowledge these things are discussed with enthusiasm, even by the public at large.

But if we are to make way with this problem special knowledge is the first need. We must know what special evidence each group of animals and plants can give, and this specialists alone can tell us. It is therefore impossible for one person to make any adequate gathering of the facts. If it is to be done it must be done by many. At one time I thought that a number of persons might perhaps be induced thus to combine; but though I hope hereafter some such organised collection may be made, it is perhaps necessary that the first trial should be single-handed. As I have thus been obliged to speak of many things of which I have no proper knowledge each section must inevitably seem meagre to those who have made its subject their special study, and I fear that many mistakes must have been made. To any one who may be willing to help to set these errors right, I offer thanks in advance, "humbly acknowledging a work of such concernment unto truth did well deserve the conjunction of many heads."

In the course of the work I have had help from so many that I cannot here give separate thanks to each. For valuable criticisms, given especially in connection with the introductory pages, I am indebted to Mr F. Darwin, Dr C. S. Sherrington, Dr D. MacAlister,

Mr W. Heape, Mr G. F. Stout, Dr A. A. Kanthack and particularly to Mr J. J. Lister. I have to thank the authorities of the British Museum, of the Museum of the Royal College of Surgeons, of the Musée d'Histoire Naturelle in Paris, and of the Museums of Leyden, Oxford, Rouen, Newcastle-upon-Tyne, of the École Vétérinaire at Alfort, and of the Dental Hospital for the great kindness that they have shown me in granting facilities for the study of their collections. In particular I must thank Mr Oldfield Thomas of the British Museum for much help and advice in connection with the subject of Teeth. I am also greatly obliged to Messrs Godman and Salvin for opportunities of examining and drawing specimens in their collections. To many others who have been good enough to lend specimens or to advise in particular cases my obligations are acknowledged in the text, but I must especially express my gratitude to Dr Kraatz of Berlin, to Dr L. von Heyden of Frankfurt, and to M. H. Gadeau de Kerville of Rouen for the large numbers of valuable insects with which they entrusted me.

My best thanks are due to Dr A. M. Norman for many useful suggestions, for the loan of specimens and for the kindly interest he has taken in my work.

My friend Mr H. H. Brindley has very kindly given me much assistance in determining and verifying several points that have arisen, and I am particularly indebted to him for permission to give an account of his very interesting and as yet unpublished observations on the variation and regeneration of the tarsus in cockroaches.

Through the help of Dr David Sharp I have been enabled to introduce much valuable evidence relating to Insects, a subject of which without his assistance I could scarcely have spoken. It is impossible for me adequately to express my obligation to Dr Sharp for his constant kindness, for the many suggestions he has given me, and for the generosity with which he has put his time and skill at my service.

It is with especial pleasure that I take this opportunity of offering my thanks to Professor Alfred Newton for the encouragement and sympathy he has given me now for many years.

As many of the subjects treated involve matters of interpretation it should be explicitly declared that though help has been given by so many, no responsibility for opinions attaches to anyone but myself unless the contrary is stated.

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The work was, as I have said, begun in the earnest hope that some may be led thereby to follow the serious study of Variation, and so make sure a base for the attack on the problems of Evolution. Those who reject the particular inferences, positive and negative, here drawn from that study, must not in haste reject the method, for that is right beyond all question.

That the first result of the study is to bring confusion and vagueness into places where we had believed order established may to some be disappointing, but it is best we deceive ourselves no longer. That the problems of Natural History are not easy but very hard is a platitude in everybody's mouth. Yet in these days there are many who do not fear to speak of these things with certainty, with an ease and an assurance that in far simpler problems of chemistry or of physics would not be endured. For men of this stamp to solve difficulties may be easy, but to feel difficulties is hard. Though the problem is all unsolved and the old questions stand unanswered, there are those who have taken on themselves the responsibility of giving to the ignorant, as a gospel, in the name of Science, the rough guesses of yesterday that tomorrow should forget. Truly they have put a sword in the hand of a child.

If the Study of Variation can serve no other end it may make us remember that we are still at the beginning, that the complexity of the problem of Specific Difference is hardly less now than it was when Darwin first showed that Natural History is a problem and no vain riddle.

On the first page I have set in all reverence the most solemn enuntiation of that problem that our language knows. The priest and the poet have tried to solve it, each in his turn, and have failed. If the naturalist is to succeed he must go very slowly, making good each step. He must be content to work with the simplest cases, getting from them such truths as he can, learning to value partial truth though he cheat no one into mistaking it for absolute or universal truth; remembering the greatness of his calling, and taking heed that after him will come Time, that "author of authors," whose inseparable property it is ever more and more to discover the truth, who will not be deprived of his due.

INTRODUCTION

All flesh is not the same flesh: but there is one kind of flesh of men, another flesh of beasts, another of fishes, and another of birds.

SECTION I

The Study of Variation

To solve the problem of the forms of living things is the aim with which the naturalist of to-day comes to his work. How have living things become what they are, and what are the laws which govern their forms? These are the questions which the naturalist has set himself to answer.

It is more than thirty years since the *Origin of Species* was written, but for many these questions are in no sense answered yet. In owning that it is so, we shall not honour Darwin's memory the less; for whatever may be the part which shall be finally assigned to Natural Selection, it will always be remembered that it was through Darwin's work that men saw for the first time that the problem is one which man may reasonably hope to solve. If Darwin did not solve the problem himself, he first gave us the hope of a solution, perhaps a greater thing. How great a feat this was, we who have heard it all from childhood can scarcely know.

In the present work an attempt is made to find a way of attacking parts of the problem afresh, and it will be profitable first to state formally the conditions of the problem and to examine the methods by which the solution has been attempted before. This consideration shall be as brief as it can be made.

The forms of living things have many characters: to solve the problem completely account must be taken of all. Perhaps no character of form is common to all living things; on the contrary their forms are almost infinitely diverse. Now in those attempts to solve the problem which have been the best, it is this diversity of form which is taken as the chief attribute, and the attempt to solve the general problem is begun by trying to trace the modes by which the diversity has been produced. In the shape in which it has been most studied, the problem is thus the problem of Species. Obscurity has been brought into the treatment of the question through want of recognition of the fact that this is really only a part of the general problem, which would still remain if there were only one species.

Nevertheless the problem of Species is so tangible a part of the whole that it is perhaps the best point of departure. For our present purpose we cannot begin better than by stating it concisely.

The forms of living things are diverse. They may nevertheless be separated into Specific Groups or Species, the members of each such group being nearly alike, while they are less like the members of any other Specific Group. [The Specific Groups may by their degrees of resemblance be arranged in Generic Groups and so on.]

The individuals of each Specific Group, though alike, are not identical in form, but exhibit differences, and in these differences they may even more or less nearly approach the form characteristic of another Specific Group. It is true, besides, that in the case of many Specific Groups which have been separated from each other, intermediate forms are found which form a continuous series of gradations, passing insensibly from the form characteristic of one Species to that characteristic of another. In such cases the distinction between the two groups for purposes of classification is not retained.

The fact that in certain cases there are forms transitional between groups which are sufficiently different to have been thought to be distinct, is a very important fact which must not be lost sight of; but though now a good many such cases are known, it remains none the less true that at a given point of time, the forms of living things may be arranged in Specific Groups, and that between the immense majority of these there are no transitional forms. There are therefore between these Specific Groups differences which are Specific.

No definition of a Specific Difference has been found, perhaps because these Differences are indefinite and hence not capable of definition. But the forms of living things, taken at a given moment, do nevertheless most certainly form a discontinuous series and not a continuous series. This is true of the world as we see it now, and there is no good reason for thinking that it has ever been otherwise. So much is being said of the mutability of species that this, which is the central fact of Natural History, is almost lost sight of, but if ever the problem is to be solved this fact must be boldly faced. There is nothing to be gained by shirking or trying to forget it.

The existence, then, of Specific Differences is one of the characteristics of the forms of living things. This is no merely subjective conception, but an objective, tangible fact. This is the first part of the problem.

In the next place, not only do Specific forms exist in Nature, but they exist in such a way as to fit the place in Nature in which they are placed; that is to say, the Specific form which an organism has, is *adapted* to the position which it fills. This again is a relative truth, for the adaptation is not absolute.

These two facts constitute the problem:

I. *The forms of living things are various and, on the whole, are Discontinuous or Specific.*

II. *The Specific forms, on the whole, fit the places they have to live in.*

How have these Discontinuous forms been brought into existence, and how is it they are thus adapted? This is the question the naturalist is to answer. To answer it completely he must find (1) *the modes* and (2) *the causes* by which these things have come to pass.

Before considering the ways in which naturalists have tried to answer these questions, it is necessary to look at some other phenomena characteristic of Life. We have said that *at a given moment*, or point of time, the specific forms of living things compose a discontinuous series. The element of time thus introduced is of consequence, and leads to important considerations. For the condition of the organised world is not a fixed condition, but changes from moment to moment, and that which can be predicated of its condition at one moment may not at any other point of time be true. This process of change is brought about partly by progressive changes in the bodies of the individuals themselves, but chiefly by the constant succession of individuals, the parents dying, their offspring succeeding them. It is then a matter of observation that the offspring born of parents belonging to any one Specific Group do as a rule conform to that Specific Group themselves, and that the form of the body, the mechanisms and the instincts of the offspring, are on the whole similar to those which their parents had. But like most general assertions about living things this is true not absolutely but relatively only. For though on the whole the offspring is like the parent or parents, its form is perhaps never identical with theirs, but generally differs from it perceptibly and sometimes materially. To this phenomenon, namely, the occurrence of differences between the structure, the instincts, or other elements which compose the mechanism of the offspring, and those which were proper to the parent, the name **Variation** has been given.

We have seen above that the two leading facts respecting the forms

of living things are first that they show specific differentiation, and secondly that they are adapted. To these we may now add a third, that in the succession from parent to offspring there is, or may be, Variation. It is upon the fact of the existence of this phenomenon of Variation that all inductive theories of Evolution have been based.

The suggestion which thus forms the common ground of these theories is this: May not the Specific Differences between Species and Species have come about through and be compounded of the individual differences between parent and offspring? May not Specific Differentiation have resulted from Individual Variation? This suggestion has been spoken of as the Doctrine of Common Descent, for it asserts that there is between living things a community of descent.

In what follows it will be assumed that this Doctrine of Descent is true. It should be admitted from the first that the truth of the doctrine has never been proved. There is nevertheless a great balance of evidence in its favour, but it finds its support not so much in direct observation as in the difficulty of forming any alternative hypothesis. The Theory of Descent involves and asserts that all living things are genetically connected, and this principle is at least not contrary to observation; while any alternative hypothesis involves the idea of Separate Creation which by common consent is now recognised as absurd. In favour of the Doctrine of Common Descent there is a balance of evidence; it is besides accepted by most naturalists; lastly if it is not true we can get no further with the problem: but inasmuch as it is unproven, it is right that we should explicitly recognise that it is in part an assumption, and that we have adopted it as a postulate.

The Doctrine of Descent being assumed, two chief solutions of the problem have been offered, both starting alike from this common ground. Let us now briefly consider each of them.

A. *Lamarck's Solution.* So many ambiguities and pitfalls are in the way of any who may try to re-state, in a few words, the theory propounded in the *Philosophie Zoologique*, that it is with great diffidence that the following account of it is given.

Lamarck points out that living things can in some measure adapt themselves both structurally and physiologically to new circumstances, and that in certain cases the adaptability is present in a high degree. He suggests that by inheritance and perfection of such adaptations

they may have become what they are, and that thus specific forms and mechanisms have been produced, as it were, by sheer force of circumstances. On this view it is assumed that to the demands made on it by the environment the organism makes an appropriate structural and physiological response; in other words, that there is in living things a certain *tension*, by which they respond to environmental pressure and fit the place they are in, somewhat as a fluid fits a vessel.

This is not, I think, a misrepresentation of Lamarck's theory. It amounts, in other words, to a proposal to regard organisms as machines which have the power of Adaptation as one of their fundamental and inherent qualities or attributes.

Without discussing this solution, we may note that it aims at being a *complete* solution of both

(1) The *existence* and *persistence* of differing forms,

(2) The fact that the differing forms are *adapted* to different conditions; and

(3) The *causes of the Variation* by which the diversity has occurred.

B. *Darwin's Solution.* Darwin, without suggesting causes of Variation, points out that since (1) Variations occur—which they are known to do—and since (2) some of the Variations are in the direction of adaptation and others are not—which is a necessity—it will result from the conditions of the Struggle for Existence that those better adapted will *on the whole* persist and the less adapted will on the whole be lost. In the result, therefore, there will be a diversity of forms, *more or less* adapted to the states in which they are placed, and this is very much the observed condition of living things.

We may note that this solution does not aim at being a complete solution like Lamarck's, for as to the *causes* of Variation it makes no suggestion.

The arguments by which these several solutions are supported, and the difficulties which are in the way of each, are so familiar that it would be unprofitable to detail them. On our present knowledge the matter is talked out. Those who are satisfied with either solution are likely to remain so.

It may be remarked however that the observed cases of adaptation occurring in the way demanded on Lamarck's theory are very few, and as time goes on this deficiency of facts begins to be significant.

Natural Selection on the other hand is obviously a "true cause," at the least.

In the way of both solutions there is one cardinal difficulty which in its most general form may be thus expressed. According to both theories, specific diversity of form is consequent upon diversity of environment, and diversity of environment is thus the ultimate measure of diversity of specific form. Here then we meet the difficulty that diverse environments often shade into each other insensibly and form a continuous series, whereas the Specific Forms of life which are subject to them on the whole form a Discontinuous Series. The immense significance of this difficulty will be made more apparent in the course of this work. The difficulty is here put generally. Particular instances have been repeatedly set forth. Temperature, altitude, depth of water, salinity, in fact most of the elements which make up the physical environment are continuous in their gradations, while, as a rule, the forms of life are discontinuous[1]. Besides this, forms which are apparently identical live under conditions which are apparently very different, while species which though closely allied are constantly distinct are found under conditions which are apparently the same. If we would make these facts accord with the view that it is diversity of environment which is the measure of diversity of specific form, it is necessary to suppose either (1) that our estimate of similarity of forms, or of environment, is wholly untrustworthy, or else (2) that there is a wide area of environmental or structural divergence within which no sensible result is produced: that is to say, that the relation between environment and structure is not finely adjusted. But either of these admissions is serious; for if we grant the former we abrogate the right of judgment, and are granting that our proposed solutions are mere hypotheses which we have no power to test; while if we admit the latter, we admit that environment cannot so far be either the directing cause or the limiting cause of Specific Differences, though the first is essential to Lamarck's Theory, and the second is demanded by the doctrine of Natural Selection.

Such then, put very briefly, are the two great theories, and this

[1] It may be objected that to any organism the other organisms coexisting with it are as serious a factor of the environment as the strictly physical components; and that inasmuch as these coexisting organisms are discontinuous species, the element of discontinuity may thus be introduced. This is true, but it does not help in the attempt to find the cause of the original discontinuity of the coexisting organisms.

is one of the chief difficulties which beset them. We must now pass to our proper work.

We have to consider whether it is not possible to get beyond the present position and to penetrate further into this mystery of Specific Forms. The main obstacle being our own ignorance, the first question to be settled is what kind of knowledge would be of the most value, and which of the many unknowns may be determined with the greatest profit. To decide this we must return once more to the ground which is common to all the inductive theories of Evolution alike. Now all these different theories start from the hypothesis that the different forms of life are related to each other, and that their diversity is due to Variation. On this hypothesis, therefore, Variation, whatever may be its cause, and however it may be limited, is the essential phenomenon of Evolution. Variation, in fact, *is* Evolution. The readiest way, then, of solving the problem of Evolution is to study the facts of Variation.

SECTION II

Alternative Methods

The Study of Variation is therefore suggested as the method which is on the whole more likely than any other to give us the kind of knowledge we are wanting. It should be tried not so much in the hope that it will give any great insight into those relations of cause and effect of which Evolution is the expression, but merely as an empirical means of getting at the outward and visible phenomena which constitute Evolution. On the hypothesis of Common Descent, the forms of living things are succeeding each other, passing across the stage of the earth in a constant procession. To find the laws of the succession it will be best for us to stand as it were aside and to watch the procession as it passes by. No amount of knowledge of individual forms will tell us the laws or even the manner of the succession, nor shall we be much helped by comparison of forms of whose descent we know nothing save by speculation. To study Variation it must be seen at the moment of its beginning. For comparison we require the parent and the varying offspring together. To find out the nature of the progression we require, simultaneously, at least two consecutive terms of the progression. Evidence of this kind can be obtained in no other way than by the study of actual and contemporary cases of Variation. To the solution of this question collateral methods of research will not contribute much.

Since Darwin wrote, several of these collateral methods have been tried, and though a great deal has thus been done and a vast number of facts have been established, yet the advance towards a knowledge of the steps by which Evolution proceeds has been almost nothing. It will not perhaps be wandering unduly if we consider very shortly the reason of this, for the need for the Study of Variation will thereby be made more plain.

Before the publication of the *Origin of Species* the work of naturalists was chiefly devoted to the indiscriminate accumulation of facts. By most the work was done for its own sake in the strictest sense. In the minds of some there was of course a hope that the gathering of knowledge would at last lead on to something more, but this hope was for the most part formless and vague. With the promulgation of the Doctrine of Descent the whole course of the study was changed. The enthusiasm of naturalists ran altogether into new channels; a new class of facts was sought and the value of Zoological discovery was judged by a new criterion. The change was thus a change of aim, and consequently a change of method. From a large field of possibilities the choice fell chiefly upon two methods, each having a definite relation to the main problem. The first of these is the Embryological Method, and the second may be spoken of as the Study of Adaptation. The pursuit of these two methods was the direct outcome of Darwin's work, and such great hopes have been set on them that before starting on a new line we shall do well to examine carefully their proper scope and see whither each of them may reasonably be expected to lead.

It is besides in the examination of these methods and in observing the exact point at which they have failed, that the need for the Study of Variation will become most evident.

When the Theory of Evolution first gained a hearing it became of the highest importance that it should be put to some test which should show whether it was true or not. In comparison with this all other questions sank into insignificance.

Now, the principle which has been called the Law of von Baer provided the means for such a test. By this principle it is affirmed that the history of the individual represents the history of the Species. If then it should be found that organisms in their development pass through stages in which they resemble other forms, this would be *primâ facie* a reason for believing them to be genetically connected. The general truth of the Theory of Descent might thus be tested by

the facts of development. For this reason the Study of Embryology superseded all others. It is now, of course, generally admitted that the Theory has stood this test, and that the facts of Embryology do support the Doctrine of Community of Descent.

But the claims of Embryology did not stop here. In addition to the application of the method to the general Theory of Descent, it has been sought to apply the facts of Embryology to solve particular questions of the descent of particular forms. It has been maintained that if it is true that the history of the individual repeats the history of the Species, we may in the study of Development see not only that the various forms are related, but also the exact lines of Descent of particular forms. In this way Embryology was to provide us with the history of Evolution.

The survey of the development of animals from this point of view is now complete for most forms of life, and in all essential points; we are now therefore in a position to estimate its value. It will, I think, before long be admitted that in this attempt to extend the general proposition to particular questions of Descent the embryological method has failed. The reason for this is obvious. The principle of von Baer was never more than a rough approximation to the truth and was never suited to the solution of particular problems. It is curious to notice upon how very slight a basis of evidence this widely received principle really rests. It has been established almost entirely by inference and it has been demonstrated by actual observation in scarcely a single instance.

For the stages through which a *particular* organism passes in the course of its development are admissible as evidence of its pedigree only when it shall have been proved as a *general* truth that the development of individuals does follow the lines on which the species developed. The proof, however, of this general proposition does not rest on direct observation but on the indirect evidence that particular organisms at certain stages in their development resemble other organisms, and hence it is assumed that they are descended from those forms. Thus the truth of the general proposition is established by assuming it true in special cases, while its applicability to special cases rests on its having been accepted as a general truth.

Probably however the apologists of this method would maintain that the principle of von Baer, though its truth has not been demonstrated directly, yet belongs to the class of "True Hypotheses." To establish the truth of a hypothesis in a case like the present in

which the number of possible hypotheses is not limited, it should at least be shown that its application in all known instances is so precise, so simple, and in such striking accordance with ascertained facts, that its truth is felt to be irresistible.

Nothing like this can be said of the principle of von Baer. Even if it be generally true that the development of a form is a record of its descent, it has never been suggested that the record is complete.

Allowance must constantly be made for the omission of stages, for the intercalation of stages, for degeneration, for the presence of organs specially connected with larval or embryonic life, for the interference of yolk and so forth. But what this allowance should be and in what cases it should be made has never been determined.

More than this: closely allied forms develop on totally different plans; for example, *Balanoglossus Kowalevskii* has an opaque larva which creeps in the sand, while the other species of the family have a transparent larva which swims at the surface of the sea; the germinal layers of the guinea-pig when compared with those of the rabbit are completely inverted, and so on. These are not isolated cases, for examples of the same kind occur in almost every group and in the development of nearly all the systems of organs. When these things are so, who shall determine which developmental process is ancestral and which is due to secondary change? By what rules may secondary changes be recognised as such? Do transparent larvæ swimming at the surface of the sea reproduce the ancestral type or does the opaque larva creeping in the mud show us the primitive form? Each investigator has answered these questions in the manner which seemed best to himself.

There is no rule to guide us in these things and there is no canon by which we may judge the worth of the evidence. It is perhaps not too much to say that the main features of the development of nearly every type of animal are now ascertained, and on this knowledge elaborate and various tables of phylogeny have been constructed, each differing from the rest and all plausible; but it would be difficult to name a single case in which the immediate pedigree of a species is actually known.

The Embryological Method then has failed not for want of knowledge of the visible facts of development but through ignorance of the principles of Evolution. The principle of von Baer, taken by itself, is clearly incapable of interpreting the phenomena of development. We are endeavouring by means of a mass of conflicting

evidence to reconstruct the series of Descent, but of the laws which govern such a series we are ignorant. In the interpretation of Embryological evidence it is constantly necessary to make certain hypotheses as to the course of Variation in the past, but before this can be done it is surely necessary that we should have some knowledge of the modes of Variation in the present. When we shall know something of the nature of the variations which are now occurring in animals and the steps by which they are now progressing before our eyes, we shall be in a position to surmise what their past has been; for we shall then know what changes are possible to them and what are not. In the absence of such knowledge, any person is at liberty to postulate the occurrence of variations on any lines which may suggest themselves to him, a liberty which has of late been freely used. Embryology has provided us with a magnificent body of facts, but the interpretation of the facts is still to seek.

The other method which, since Darwin's work, has attracted most attention is the study of the mechanisms by which organisms are adapted to the conditions in which they live. This study of Adaptation and of the utility of structures exercises an extraordinary fascination over the minds of some and it is most important that its proper use and scope should be understood.

We have seen that the Embryological Method owed its importance to its value as a mode of testing the truth of the Theory of Evolution: in the same way the Study of Adaptation was undertaken as a test of the Theory of Natural Selection.

Amongst many classes of animals, complex structures are present which do not seem to contribute directly to the well-being of their possessors. By many it has been felt that the persistent occurrence of organs of this class is a difficulty, on the hypothesis that there is a tendency for useful structures to be retained and for useless parts to be lost. In consequence it has been anticipated that sufficient research would reveal the manner in which these parts are directly useful. The amount of evidence collected with this object is now enormous, and most astonishing ingenuity has been evoked in the interpretation of it. A discussion of the truth of the conclusions thus put forward is of course apart from our present purpose, which is to examine the logical value of this method of research as a means of attacking the problem of Evolution. With regard to the results it has attained it must suffice to notice the fact that while the functions of

many problematical organs have been conjectured, in some cases perhaps rightly, there remain whole groups of common phenomena of this kind, which are still almost untouched even by speculation, and structures and instincts are found in the best known forms, as to the "utility" of which no one has made even a plausible surmise. All this is familiar to every one and every one knows the various answers that have been made.

It is not quite fair to judge such a method by the imperfection of its results, but in one respect the deficiency of results obtained by the Study of Adaptation is very striking, and though this has often been recognised it must be again and again insisted on as a thing to be kept always in view. The importance of this consideration will be seen when the evidence of Variation is examined. The Study of Adaptation ceases to help us at the exact point at which help is most needed. We are seeking for the cause of the differences between species and species, and it is precisely on the utility of Specific Differences that the students of Adaptation are silent. For, as Darwin and many others have often pointed out, the characters which visibly differentiate species are not as a rule capital facts in the constitution of vital organs, but more often they are just those features which seem to us useless and trivial, such as the patterns of scales, the details of sculpture on chitin or shells, differences in number of hairs or spines, differences between the sexual prehensile organs and so forth. These differences are often complex and are strikingly constant, but their utility is in almost every case problematical. For example, many suggestions have been made as to the benefits which edible moths may derive from their protective coloration, and as to the reasons why unpalatable butterflies in general are brightly coloured; but as to the particular benefit which one dull moth enjoys as the result of his own particular pattern of dullness as compared with the closely similar pattern of the next species, no suggestion is made. Nevertheless these are exactly the real difficulties which beset the utilitarian view of the building up of Species. We knew all along that Species are *approximately* adapted to their circumstances; but the difficulty is that whereas the differences in adaptation seem to us to be approximate, the differences between the structures of species are frequently precise. In the early days of the Theory of Natural Selection it was hoped that with searching the direct utility of such small differences would be found, but time has been running now and the hope is unfulfilled.

Even as to the results which rank among the triumphant successes of this method of study there is need for great reserve. The adequacy of such evidence must necessarily be a matter for individual judgment, but in dealing with questions of Adaptation more than usual caution is needed. No disrespect is intended towards those who have sought to increase our acquaintance with these obscure phenomena; but since at the present time the conclusions arrived at in this field are being allowed to pass unchallenged to a place among the traditional beliefs of Science, it is well to remember that the evidence for these beliefs is far from being of the nature of proof.

The real objection however to the employment of the Study of Adaptation as a means of discovering the processes of Evolution is not that its results are meagre and its conclusions unsound. Apart from the doubtful character of these inferences, there is a difficulty of logic which in this method is inherent and insuperable. This difficulty lies in the fact that while it is generally possible to suggest some way by which in circumstances, known or hypothetical, any given structure may be of use to any animal, it cannot on the other hand ever be possible to prove that such structures are not on the whole harmful either in a way indicated or otherwise. There is a special reason why the impossibility of proving the negative applies with peculiar force to the mode of reasoning we are now considering. This is due to the fact that whereas the only possible test of the utility of a structure must be a quantitative one, such a quantitative method of assessment is entirely beyond our powers and is likely to remain so indefinitely. The students of Adaptation forget that even on the strictest application of the theory of Selection it is unnecessary to suppose that every part an animal has, and every thing which it does, is useful and for its good. We, animals, live not only by virtue of, but also in spite of what we are. It is obvious from inspection that any instinct or any organ *may* be of use: the real question we have to consider is of *how much* use it is. To know that the presence of a certain organ *may* lead to the preservation of a race is useless if we cannot tell how much preservation it can effect, how many individuals it can save that would otherwise be lost; unless we know also the degree to which its presence is harmful; unless, in fact, we know how its presence affects the profit and loss account of the organism. We have no right to consider the utility of a structure *demonstrated*, in the sense that we may use this demonstration as evidence of the causes which have led to the existence of the struc-

ture, until we have this quantitative knowledge of its utility and are able to set off against it the cost of the production of the structure and all the difficulties which its presence entails on the organism. No one who has ever tried to realise the complexity of the relations between an organism and its surroundings, the infinite variety of the consequences which every detail of structure and every shade of instinct *may* entail upon the organism, the precision of the correlation between function and the need for it, and above all the marvellous accuracy with which the presence or absence of a power or a structure is often compensated among living beings—no one can reflect upon these things and be hopeful that our quantitative estimates of utility are likely to be correct. But in the absence of such correct and final estimates of utility, we must never use the *utility* of a structure as a point of departure in considering the manner of its origin; for though we can see that it is, or may be, useful, yet a little reflection will show that it is, or may be, harmful, but whether on the whole it is useful or on the whole harmful can only be guessed at. It thus happens that we can only get an indefinite knowledge of Adaptation, which for the purposes of our problem is not an advance beyond the original knowledge that organisms are all *more or less* adapted to their circumstances. No amount of evidence of the same kind will carry us beyond this point. Hence, though the Study of Adaptation will always remain a fascinating branch of Natural History, it is not and cannot be a means of directly solving the problem of the origin of Species.

SECTION III

Continuity or Discontinuity of Variation

What is needed, then, is evidence of a new kind, for no amount of evidence of the kinds that have been mentioned will take us much beyond our present position. We need more knowledge, not so much of the facts of anatomy or development, as of the principles of Evolution. The question to be considered is how such knowledge may be obtained. It is submitted that the Study of Variation gives us a chance, and perhaps the only one, of arriving at this knowledge.

But though, as all will admit, a knowledge of Variation lies at the root of all biological progress, no organised attempt to obtain it has been made. The reason for this is not very clear, but it apparently proceeds chiefly from the belief that the subject is too difficult and

complex to be a profitable field for study. However this may be, the fact remains, that since the first brief treatment of the matter in *Animals and Plants under Domestication* no serious effort to perceive or formulate principles of Variation has been made, and there is before us nothing but the most meagre and superficial account of a few of its phenomena. Darwin's first collection of the facts of Variation has scarcely been increased. These same facts have been arranged and rearranged by each successive interpreter; the most various and contradictory propositions have been established upon them, and they have been strained to show all that it can possibly be hoped that they will show. Any one who cares to glance at the works of those who have followed Darwin in these fields may assure himself of this. So far, indeed, are the interpreters of Evolution from adding to this store of facts, that in their hands the original stock becomes even less until only the most striking remain. It is wearisome to watch the persistence with which these are revived for the purpose of each new theorist. How well we know the offspring of Lord Morton's mare, the bitch "Sappho," the Sebright Bantams, the Himalaya rabbit with pink eyes, the white cats with their blue eyes, and the rest! Perhaps the time has come when even these splendid observations cannot be made to show much more. Surely their use is now rather to point the direction in which we must go for more facts.

The questions which by the Study of Variation we hope to answer may be thus expressed. In affirming our belief in the doctrine of the Community of Descent of living things, we declare that we believe all living things to stand to each other in definite genetic relationships. If then all the individuals which have lived on the earth could be simultaneously before us, we believe that it would be possible to arrange them all, so that each stood in its own ordinal position in series. We believe that all the secondary series together make up one primary series from which each severally arises. This is the fundamental conception of Evolution and is represented figuratively by the familiar image of a genealogical tree. If then all the individual ancestors of any given form were before us and were arranged in their order, we believe they would constitute a series. This view of the forms of organisms as constituting a series or *progression* is the central idea of modern biology, and must be borne continually in mind in the attempt to apply any principle to the Study of Evolution.

Each individual and each type which exists at the present moment

stands, for the moment, therefore, as the last term of such a series. The problem is to find the other terms. In the case of each type the question is thus stated in a particular form, and it is a somewhat remarkable circumstance that it is in its particular forms that this problem has been most studied. The same problem is nevertheless capable of being stated in the general form also. Instead of considering what has been the actual series from which a specified type has been derived, we may consider what are the characters and attributes of such series in general. It may indeed be contended that it is scarcely reasonable to expect to discover the line of descent of a given form, for the evidence is gone; but we may hope to find the general characteristics of Evolution, for Evolution, as we believe, is still in progress. It is really a strange thing that so much enterprise and research should have been given to the task of reconstructing particular pedigrees—a work in which at best the facts must be eked out largely with speculation—while no one has ever seriously tried to determine the general characters of such a series. Yet if our modern conception of Descent is a right one, it is a phenomenon now at this time occurring, which by common observations, without the use of any imagination whatever, we may now see. The chief object, then, with which we shall begin the Study of Variation will be the determination of the nature of the Series by which forms are evolved.

The first questions that we shall seek to answer refer to the manner in which differentiation is introduced in these Series. All we as yet know is the last term of the Series. By the postulate of Common Descent we take it that the first term differed widely from the last, which nevertheless is its lineal descendant: how then was the transition from the first term to the last term effected? If the whole series were before us, should we find that this transition had been brought about by very minute and insensible differences between successive terms in the Series, or should we find distinct and palpable gaps in the Series? In proportion as the transition from term to term is minimal and imperceptible we may speak of the Series as being **Continuous,** while in proportion as there appear in it lacunæ, filled by no transitional form, we may describe it as **Discontinuous.** The several possibilities may be stated somewhat as follows. The Series may be wholly continuous; on the other hand it may be sometimes continuous and sometimes discontinuous; we know however by common knowledge that it is never wholly discontinuous. It may be that through long periods of the Series the differences between each

member and its immediate predecessor and successor are impalpable, while at certain moments the series is interrupted by breaches of continuity which divide it into groups, of which the composing members are alike, though the successive groups are unlike. Lastly, discontinuity may occur in the evolution of particular organs or particular instincts, while the changes in other structures and systems may be effected continuously. To decide which of these agrees most nearly with the observed phenomena of Variation is the first question which we hope, by the Study of Variation, to answer. The answer to this question is of vital consequence to progress in the Study of Life.

The preliminary question, then, of the degree of continuity with which the process of Evolution occurs, has never been decided. In the absence of such a decision there has nevertheless been a common assumption, either tacit or expressed, that the process is a continuous one. The immense consequence of a knowledge of the truth as to this will appear from a consideration of the gratuitous difficulties which have been introduced by this assumption. Chief among these is the difficulty which has been raised in connection with the building up of new organs in their initial and imperfect stages, the mode of transformation of organs, and, generally, the Selection and perpetuation of minute Variations. Assuming then that Variations are minute, we are met by this familiar difficulty. We know that certain devices and mechanisms are useful to their possessors; but from our knowledge of Natural History we are led to think that their usefulness is consequent on the degree of perfection in which they exist, and that if they were at all imperfect, they would not be useful. Now it is clear that in any continuous process of Evolution such stages of imperfection must occur, and the objection has been raised that Natural Selection cannot protect such imperfect mechanisms so as to lift them into perfection. Of the objections which have been brought against the Theory of Natural Selection this is by far the most serious.

The same objection may be expressed in a form which is more correct and comprehensive. We have seen that the differences between Species on the whole are Specific, and are differences of kind, forming a discontinuous Series, while the diversities of environment to which they are subject are on the whole differences of degree, and form a continuous Series; it is therefore hard to see how the environmental differences can thus be in any sense the directing cause of Specific differences, which by the Theory of Natural Selection they

should be. This objection of course includes that of the utility of minimal Variations.

Now the strength of this objection lies wholly in the supposed continuity of the process of Variation. We see all organised nature arranged in a discontinuous series of groups differing from each other by differences which are Specific; on the other hand we see the divers environments to which these forms are subject passing insensibly into each other. We must admit, then, that if the steps by which the divers forms of life have varied from each other have been insensible —if in fact the forms ever made up a continuous series—these forms cannot have been broken into a discontinuous series of groups by a continuous environment, whether acting directly as Lamarck would have, or as selective agent as Darwin would have. This supposition has been generally made and admitted, but in the absence of evidence as to Variation it is nevertheless a gratuitous assumption, and as a matter of fact when the evidence as to Variation is studied, it will be found to be in great measure unfounded.

In what follows so much will be said of discontinuity in Variation that it will not be amiss to speak of the reasons which have led many to suppose that the continuity of Variation needs no proof. Of these reasons there are especially two. First there is in the minds of some persons an inherent conviction that *all* natural processes are continuous. That many of them do not appear so is admitted: it is admitted, for example, that among chemical processes Discontinuity is the rule; that changes in the states of matter are commonly effected discontinuously, and the like. Nevertheless it is believed that such outward and visible Discontinuity is but a semblance or mask which conceals a real process which is continuous and which by more searching may be found. With this class of objections we are not perhaps concerned, but they are felt by so many that their existence must not be forgotten. Secondly, Variation has been supposed to be always continuous and to proceed by minute steps because changes of this kind are so common in Variation. Hence it has been inferred that the mode of Variation thus commonly observed is universal. That this inference is a wrong one, the facts will show.

To sum up:

The first question which the Study of Variation may be expected to answer, relates to the origin of that Discontinuity of which Species is the objective expression. Such Discontinuity is not in the environment; may it not, then, be in the living thing itself?

The Study of Variation thus offers a means whereby we may hope to see the processes of Evolution. We know much of what these processes *may* be: the deductive method has been tried, with what success we know. It is time now to try if these things cannot be seen as they are, and this is what Variation may show us. In Variation we look to see Evolution rolling out before our eyes. In this we may fail wholly and must fail largely, but it is still the best chance left.

SECTION IV

Symmetry and Meristic Repetition

Having thus indicated some of the objects which we may hope to reach by the Study of Variation, we have next to consider the way in which to set about this study.

The Study of Variation is essentially a study of differences between organisms, so for each observation of Variation at least two substantive organisms are required for comparison. It is proposed to confine the present treatment of the subject to a consideration of the integral steps by which Variation may proceed; hence it is desirable that the two organisms compared should be parent and offspring, and if, as is often the case, the actual parent is unknown, it is at least necessary that the normal form of the species should be known and that there must be reasonable evidence that the varying offspring is actually descended from such a normal. For this reason, evidence from a comparison of Local Races, and other established Varieties, though a very valuable part of the Study, will for the most part not be here introduced. For the belief that such races are descended from the putative normal scarcely ever rests on proof, and still more rarely is there evidence of the number of generations in which the change has been effected.

For our purpose we require actual cases of Variations occurring as far as possible in offspring of known parentage; and if, failing this, we make use of cases occurring in the midst of normal individuals of known structure, it must in such cases be always remembered that we cannot properly assume that the varying form is the offspring of such individuals, though special reasons may make this likely in special cases.

Since the structure of the offspring is perhaps in no case identical with that of the parent, observation of any parent and its offspring

is to the point; but such a field as this is plainly too wide to be studied with profit as a whole, and it is necessary from the first that attention should be limited to certain classes of such phenomena. With this object certain limitations are proposed, and though confessedly arbitrary, they will be found on the whole to work well.

The first limitation thus introduced concerns the *magnitude* of Variations. We have seen above that the assumption that Variation is a continuous process lands us in serious difficulties in the application of a hypothesis which, on general grounds, we nevertheless are prepared to receive. If then we can show that Variation is to some extent discontinuous, a road will be opened by which these difficulties may perhaps be in part avoided.

Species are discontinuous; may not the Variation by which Species are produced be discontinuous too? It may be stated at once that evidence of such Discontinuous Variation does exist, and in this first consideration of the subject attention will be confined to it. The fact that Continuous Variation exists is also none the less a fact, but it is most important that the two classes of phenomena should be recognised as distinct, for there is reason to think that they are distinct essentially, and that though both may occur simultaneously and in conjunction, yet they are manifestations of distinct processes. The attempt to distinguish these two kinds of Variation from each other constitutes one of the chief parts of the study. It will not perhaps be possible to find any general expression which shall accurately differentiate between Variations which are Discontinuous and those which are Continuous, but it is possible to recognise attributes proper to each and to distinguish changes which are or may be effected in the one way from other changes which are or may be effected in the other.

For the present we shall treat only of the evidence of Discontinuous Variation.

In order to explain the second limitation which is to be introduced it is necessary to refer to some phenomena which are characteristic of the forms of organisms, and to separate from them the group with which we shall deal first.

It was stated above that perhaps no character of form is common to all living things, but nevertheless there is one feature which is found in the great majority.

In the first place, the bodies of organisms are not homogeneous but

heterogeneous, consisting of organs or parts which in substance and composition differ from each other. This heterogeneity in composition is of course an objective expression of the process of Differentiation, and it is further recognised that such structural heterogeneity of material corresponds with a physiological Differentiation of function. This differentiation or Heterogeneity is found in the bodies of all organisms, even in the simplest.

Now in a wide survey of the forms of living things there is a fact with regard to the presence of this Heterogeneity which to the purpose of our present consideration is of the highest consequence. This may perhaps be best expressed by the statement that in the bodies of living things Heterogeneity is generally orderly and formal; it is cosmic, not chaotic. Not only are the bodies of all organisms heterogeneous, but in the great majority the Heterogeneity occurs in a particular way and according to geometrical rule. This character is not peculiar to a few organisms, but is common to nearly all. We will now examine this phenomenon of geometrical order in Heterogeneity and try to see some of the elements of which it is made up.

Order of form will first be found to appear in the fact that in any living body the Heterogeneity is in some degree symmetrically distributed around one or more centres. In the great majority of instances these centres of symmetry are themselves distributed about other centres, so that in one or more planes the whole body is symmetrical.

The idea of **Symmetry** which is here introduced is so familiar that it is scarcely necessary to define it, but as all that follows depends entirely on the proper apprehension of what is meant by Symmetry it may be well to call attention to some of the phenomena which the term denotes.

In its simplest form the Symmetry of a figure depends on the fact that from some point within it at least two lines may be taken in such a way that each passes through parts which are similar and similarly disposed. The point from which the lines are taken may be called a centre of Symmetry and the lines may be called lines of Symmetrical Repetition.

Commonly the parts thus symmetrically disposed are related to each other as optical images [in a plane mirror passing through the centre of Symmetry and standing in a plane bisecting the angle which the lines of Symmetrical Repetition make with each other]. For a figure to be symmetrical, in the ordinary sense of the term, it is not

necessary that the relation of optical images should strictly exist, and several figures, such as spirals, etc., are accordingly described as symmetrical. But since the relation of images exists in all cases of bilateral and radial symmetry, which are the forms most generally assumed in the symmetry of organisms, it is of importance to refer particularly to this as one of the phenomena often associated with Symmetry.

In the simplest possible case of Symmetry there is a series of parts in one direction corresponding to a series of parts in another direction. Perhaps there is no organism in which such an arrangement does not at some time and in some degree exist. For even in an unsegmented ovum or a resting *Amœba* there is little doubt that Symmetry is present, though owing to the slight degree of Differentiation, its presence may not be clearly perceived. In the manifestations, however, in which it is most familiar, Symmetry is a decided and obvious phenomenon.

Symmetry then depends essentially on the fact that structures found in one part of an organism are repeated and occur again in another part of the same organism. Symmetrical Heterogeneity may therefore be present in a spherical body having a core of different material, and it is possible that in an unsegmented ovum for example a Symmetry of this simple kind may exist. But Symmetry, as it is generally seen in organisms, differs from that of these simplest cases in the fact that the organs repeated are separated from each other by material of a nature different from that of the organs separated. Repetitions of this kind are known in almost every group of animals and plants. The parts thus separated may belong to any system of organs. There is no known limit to the number of Repetitions that may occur.

This phenomenon of Repetition of Parts, generally occurring in such a way as to form a Symmetry or Pattern, comes near to being a universal character of the bodies of living things. It will in cases which follow be often convenient to employ a single term to denote this phenomenon wherever and however occurring. For this purpose the term **Merism** will be used. The introduction of a new term is, as a practice, hardly to be justified; but in a case like the present, in which it is sought to associate divers phenomena which are commonly treated as distinct, the employment of a single word, though a new one, is the readiest way of giving emphasis to the essential unity of the phenomena comprised.

The existence of patterns in organisms is thus a central fact of morphology, and their presence is one of the most familiar characters of living things. Anyone who has ever collected fossils, or indeed animals or plants of any kind, knows how in hunting the eye is caught by the formal regularity of an organised being, which, contrasting with the irregularity of the ground, is often the first indication of its presence. Though of course not diagnostic of living things, the presence of patterns is one of their most general characters.

On examining more closely into the constitution of Repetitions, they may be seen to occur in two ways; first, by Differentiation within the limits of a single cell, as in the *Radiolaria*, the sculpture of egg-shells, nuclear spindles, etc., to take marked cases; and secondly, by, or in conjunction with, the process of Cell-Division. The Symmetry which is found in the Serial Repetitions of Parts in unicellular organisms does not in all probability differ essentially from that which is produced by Cell-Division, for, though sufficiently distinct in outward appearance, the two are almost certainly manifestations of the same power.

Such patterns may exist in single cells or in groups of cells, in separate organs or in groups of organs, in solitary forms or in colonies and groups of forms. Patterns which are completed in the several organs or parts will be referred to as **Minor Symmetries.** These may be compounded together into one single pattern, which includes the whole body: such a symmetry will be called a **Major Symmetry.** In most organisms, whether colonial or solitary, there is such a Major Symmetry; on the other hand organisms are known in which each system of Major Symmetry is, at least in appearance, distinct and without any visible geometrical relation to the other Minor Symmetries. Examples of this kind are not common, for, as a rule, the planes about which each Minor Symmetry is developed have definite geometrical relations to those of the other Minor Symmetries. It is possible, even, that in some if not all of these, the planes of division by which the tissues composing each system of Minor Symmetry are originally split off and differentiated, have such definite relations, though by subsequent irregularities of growth and movement these relations are afterwards obscured.

The classification of Symmetry and Pattern need not now be further pursued. The matter will be often referred to in the course of this work, when facts concerning Variations in number and patterns are being given, for it is by study of Variations in pattern and in

repetition of parts that glimpses of the essential phenomena of Symmetry may be gained.

That which is important at this stage is to note the almost universal presence of Symmetry and of Repetition of Parts among living things. Both are the almost invariable companions of division and differentiation, which are fundamental characters without which Life is not known.

The essential unity of the phenomenon of Repetition of Parts and of its companion-phenomenon, Symmetry, wherever met with, has been too little recognised, and needless difficulty has thus been introduced into morphology. To obtain a grasp of the nature of animal and vegetable forms, such recognition is of the first consequence.

To anyone who is accustomed to handle animals or plants, and who asks himself habitually—as every Naturalist must—how they have come to be what they are, the question of the origin and meaning of patterns in organisms will be familiar enough. They are the outward and visible expression of that order and completeness which inseparably belongs to the phenomenon of Life.

If anyone will take into his hand some complex piece of living structure, a passion-flower, a peacock's feather, a cockle-shell, or the like, and will ask himself, as I have said, how it has come to be so, the part of the answer that he will find it hardest to give is that which relates to the perfection of its pattern.

And it is not only in these large and tangible structures that the question arises, for the same challenge is presented in the most minute and seemingly trifling details. In the skeleton of a Diatom or of a Radiolarian, the scale of a butterfly, the sculpture on a pollen-grain or on an egg-shell, in the wreaths and stars of nuclear division, such patterns again and again recur, and again and again the question of their significance goes unanswered. There are many suggestions, some plausible enough, as to why the tail of a peacock is gaudy, why the coat of a pollen-grain should be rough, and so forth, but the significance of patterns is untouched by these. Nevertheless, repetitions arranged in pattern exist throughout organised Nature, in creatures that move and in those that are fixed, in the great and in the small, in the seen and in the hidden, within and without, as a property or attribute of Life, scarcely less universal than the function of respiration or metabolism itself.

Such, then, is Symmetry, a character whose presence among organisms approaches to universality.

SECTION V

Meristic Variation and Substantive Variation

It is to the origin and nature of Symmetry that the first section of the evidence of Variation will relate. That a knowledge of the modes of Variation of so universal a character is important to the general study of Biology must at once be evident, but to the particular problem of the nature of Specific Differences this importance is immense. This special importance comes from two reasons. As it is the fact first that Repetition and Symmetry are among the commonest features of organised structure, so it will be found next that it is by differences in those features that the various forms of organisms are very commonly differentiated from each other. Their forms are classified by all sorts of characters, by shape and proportions, by size, by colour, by habits and the like; but perhaps almost as frequently as by any of these, by differences in number of parts and by differences in the geometrical relations of the parts. It is by such differences that the larger divisions, genera, families, etc., are especially distinguished. In such cases of course the differences in number and Symmetry do not as a rule stand alone, but are generally, and perhaps always, accompanied by other differences of a qualitative kind; nevertheless, the differences in number and Symmetry form an integral and very definite part of the total differences, so that in any consideration of the nature of the processes by which the differences have arisen, special regard must be had to these numerical and geometrical, or, as I propose to call them, **Meristic**, changes.

In the present Introduction I do not propose to forestall the evidence more than is absolutely necessary for the purpose of making clear the principles on which the facts are grouped, but it will do the evidence no wrong if at the present stage it is stated that Meristic Variation is frequently Discontinuous, and in the case of certain classes of Repetitions is perhaps always so.

The nature of Merism and the manner in which Meristic Variations occur will be fully illustrated hereafter, but it is necessary to say this much at the present stage, since it is from this Discontinuity in the occurrence of Meristic Variations that the phenomena of Symmetry and Repetition derive their special importance in the Study of Variation.

The importance of the phenomena of Merism to the Study of Variation is thus, in the first instance, a direct one, for the Variations which have resulted in the production of Meristic Systems are a direct factor in Evolution. In addition to this direct relation to the Study of Variation, the phenomena of Merism have also an indirect relation, which is scarcely less important; for they are a factor in the estimation of the magnitude of the integral steps by which Variation proceeds. This will be more evident after the second group of Variations has been spoken of.

We have thus far spoken only of the processes by which the living body is divided into parts, and we have thus constituted a group which is to include Variations in number, Division, and geometrical position. From these phenomena of Division may be distinguished Variations in the actual constitution or substance of the parts themselves. To these Variations the name **Substantive** will be given. Under this head several phenomena may be temporarily grouped together, which with further knowledge will doubtless be found to have no real connection with each other. For the present, however, it will be convenient to constitute such a temporary group in order to bring out the relative distinctness of Variations which are Meristic.

These two classes of Variation, Meristic and Substantive, may be recognised at the outset of the study. There can be no doubt that they are essentially distinct from each other, and the proof that they are thus distinct will be found in the evidence of Variation, for it will be seen that either may occur independently of the other. An appreciation of this distinction is a first step towards a comprehension of the processes by which the bodies of organisms are evolved.

A few simple illustrations may make the nature of these two classes of Variations more clear. For example, then, the flower of a *Narcissus* is commonly divided into six parts, but through Meristic Variation it may be divided into seven parts or into only four. Nevertheless there is in such a case no perceptible change in the tissues or substance of which the parts are made up. All belong to and are recognisable as belonging to the same sort of *Narcissus*. On the other hand many *Narcissi*, *N. corbularia*, for example, are known in two colours, one a dark yellow and the other a sulphur-yellow, though the number of parts and pattern of the flowers are identical. This is, therefore, an example of a Substantive Variation.

Again, the foot of a pig may, through Meristic Variation, be divided into five or six toes instead of into four; or, on the other hand, the number may, by absence of the median division between the digits III and IV, be reduced to three, though the tissues composing the toes may not in structure differ from the normal.

Again, the tarsus of a cockroach (*Blatta*) may, through Meristic Variation, be divided into only four joints instead of into five, the normal number, but the joints are still in substance or quality those of a cockroach.

I am aware that Meristic and Substantive Variations often occur together, and that there is a point at which it is not possible to separate satisfactorily the changes which have come about by the one process from those which have come about by the other. Instances of this kind occur especially in the case of series of parts such as teeth or vertebræ, in which individual members or groups of members of the series are differentiated from the others. For example, we may see that it is through Meristic Variation that the vertebral column of a dog may be divided into a number of vertebræ greater or less than the normal; and though in such cases all the vertebræ have distinctively canine characters, yet there are nearly always Substantive Variations occurring in correlation with the Meristic Variations, manifesting themselves in a re-arrangement of the points of division between the several groups of vertebræ, and causing individual vertebræ to assume characters which are not proper to their ordinal positions.

Further inquiry into the questions thus raised cannot at this stage be profitably undertaken, though when the evidence has been considered it will perhaps be advisable to recur to them; all that is now intended is to indicate broadly the general scope of Meristic and Substantive Variation respectively.

As has already been stated, it is proposed to begin the Study of Variation by an examination of Variations which are Meristic, leaving the consideration of Substantive Variation to be undertaken hereafter. But nevertheless in the consideration of Meristic Variation it will be necessary to refer to phenomena of Substantive Variation in so far as their occurrence or distribution in the body are affected by Meristic phenomena. For in the determination of the magnitude of the integral steps by which Variation proceeds, the existence of Merism plays a conspicuous part, and it is in consequence of this that the subject of Symmetry and Repetition of Parts has a second and

indirect bearing on the Study of Variation which is scarcely less important than the direct bearing of which mention has been made above.

This indirect bearing on the manner of origin of Specific Differences arises from a circumstance which in treatises on Evolution is commonly overlooked. In comparing a species in which parts are repeated with an allied species in which the same parts are repeated, it commonly occurs that each of the repeated parts of the one have some character by which they are distinguished from the like parts of the other. This differentiating character may be a qualitative one, or a numerical one, or both. In such cases it very frequently happens that this character occurs in each member of the series of Repetitions. For example, the tarsi of the weevils have only four visible joints, while those of the majority of beetles have five; but the characteristic division into four joints occurs in each of the legs. Before the four-jointed character as seen in the weevils could be produced it was necessary that not one but all of the legs should vary from the five-jointed form, and in this particular way. The leaves on a beech tree are all beech leaves, and if the tree is a fern-leaved beech they *may*, and generally speaking do, all show the characters of that variety; and so on with other particular species and varieties.

The limbs of a bilaterally symmetrical animal, in which the right side is the image of the left, are of course alike, and any specific character which is present in the limbs of the one side must in such an animal be normally present in those of the other side.

The same is true of many forms in which appendages are repeated in series, as for example the fore-legs and hind-legs of the horse, the fore- and hind-wings of the Brimstone butterfly (*Gonepteryx rhamni*); of the patterns on several segments of many caterpillars; of the patterns of the segmental setæ of many worms, and so forth. In series whose members are differentiated from each other, it of course frequently happens that the same specific characters are not present in all the members of the series, and in nearly all such cases these characters are not presented by all in equal degree; nevertheless substantially the phenomenon remains that similar characters often are presented by the several members of a series of repeated organs.

To many this will seem little better than a truism, nevertheless I offer no apology for its introduction; for though, as a common and obvious fact, it is a truism, it is besides a truth, the far-reaching significance of which is scarcely appreciated. For, in the consideration of the magnitude of the integral steps by which Variation proceeds,

we shall have this to remember: that to produce any of the forms of which we have spoken, by Variation from another form, it is not enough that the particular Variation should occur and become fixed in one member of the series, but it is necessary that the character should sooner or later be taken on by *each* member of the series which exhibits it. In such cases, therefore, this question is raised. Did the Variation come in first in one member of the Series and then in another? Did it occur, for example, simultaneously on the two sides of the body? Did the right and left fore-legs of the horse cease to develop more than the present number of digits simultaneously or separately? Was the similar form of the hind-legs assumed before, after, or simultaneously with that of the fore-legs? Were the orange markings which are present on both fore- and hind-wings of the Brimstone, or the ocellar markings of the Peacock (*V. Io*), and of the Emperor (*Saturnia carpini*) assumed by both wings at once? Were the four wings of the Plume moths split simultaneously into the characteristic "plumes"? Did the brown spots on the three leaflets of *Medicago*, the fimbriation of the petals of ragged robin (*Lychnis flos-cuculi*), the series of stripes on the zebra, the pink slashes on the segments of *Sphinx* larvae, the eyes on the scutes of chitons, and the thousand other colour-marks, sense-organs, appendages and structural features, which throughout organised Nature occur in Series, vary to their present state of similarity by similar and simultaneous steps, or did each member of such Series take these characters by steps which were separate and occurring independently? To this question, which lies at the root of all progress in the knowledge of Evolution, the Study of Variation can alone reply. That in the facts which follow, the answer to this question will be found, cannot of course be said; but these facts, few though they are, do nevertheless answer it in part, and they suggest that more facts of the same kind would go far towards answering it completely. But beyond this, the facts are of value as an indication of the part which the phenomenon of Merism may play in determining the magnitude of Variations and the manner of their distribution among the several parts of the body. On examining the evidence it will be found that between parts related to each other in the way that has been described, there is a certain bond or kinship, by virtue of which they *may* and often do vary simultaneously and in similar ways, though the fact that they may also vary independently, and in different ways, will of course also appear.

The phenomenon of the Similar Variation of parts which are repeated Meristically in Series is a fact which will be found to have important bearings on several distinct departments of biological study.

As was shown above, it is by recognition of the existence of such similar and simultaneous Variation that the manner of origin of the similar complexity of several organs belonging to the same system or series becomes comparatively comprehensible; for it is not then necessary to conceive a separate origin for the complexity of each member of the series. For example, it is difficult to conceive the manner of evolution of an eye of a vertebrate; nevertheless, for each vertebrate *two* eyes have been evolved. If it were necessary to suppose that each arose by separate selections of separate Variations, the difficulty would be thus doubled. If, however, it is recognised that the complexity of both arose simultaneously, the phenomenon becomes the more intelligible as the number of integral Variations and selections demanded is reduced.

The case chosen, of paired organs in bilateral symmetry, is a very simple one, but it will be found that similar relations hold between other parts repeated in series. For in the same way it is not necessary to suppose an independent evolution for each of the tail-feathers of the peacock, for the legs of the horse, and the like, since in the light of the facts of Variation it is as easy for all to take on the new characters as for one.

If the manner of development of Repeated Parts is considered, this fact will not seem surprising. For all these parts arise from the undifferentiated tissues by a process of Division, and whatever characters were potentially present in the undifferentiated tissues may appear in the parts into which it subsequently divides. A somewhat loose illustration will perhaps make this more clear. Everyone knows the rows of figures which children cut out from folded paper. There are as many figures as folds, each figure being alike if the folds coincide. If the paper is pink, all the figures are pink; if the paper is white, all the figures are white, and so on. If blotting-paper is used, and one blot is dropped on the folded edges, the blot appears symmetrically in all the figures. So also any deviation in the lines of cutting appears in all the figures; a whole row of soldiers in bearskins may be put into helmets by one stroke of the scissors. Of course it is not meant to suggest that the process of division by which parts of the body are produced bears any resemblance to that by which the figures are cut out, but merely to illustrate the fact that since it is

by a process of Division of an undifferentiated mass that the Repeated Parts are produced, so the characters of these Repeated Parts depend upon the characters which were present in the original mass and upon the modes by which the parts were divided out from it.

Summary of Sections I to V

At this point it will be well briefly to recapitulate the preceding Sections.

We are proposing to attack the problem of Species by studying the facts of Variation. Of the facts of Variation in general we have selected a particular group upon which to begin this study. The group of Variations thus chosen are those which relate to Number of parts, Division, Repetition, and the other phenomena which are to be included under the term Meristic. With Variations in quality and substance it is not at present proposed to deal, except in so far as it is necessary to refer to them in their relation to the phenomena of Merism, and in illustration of the structural possibilities or necessities which in the body follow as corollaries upon the existence of Meristic Repetition.

It has also been proposed to limit the consideration to Variations which are Discontinuous. As has been already stated, Discontinuous Variations may belong to the Meristic Group or to the Substantive, but it is to the former that attention will first be directed.

SECTION VI

Meristic Repetition and Homology

In what has gone before, the two conceptions now introduced, namely the distinction of Variations into Meristic and Substantive, and into Continuous and Discontinuous, have been sketched in outline. The significance of the facts which follow will be made more evident if these two conceptions are now more fully developed in some of their aspects.

Under the name Merism I have proposed to include all phenomena of Repetition and Division, whenever found and in whatever forms occurring, whether in the parts of a body or in the whole. The consequences of the admission of this proposition are considerable and should be fully realised; for on recognition of the unity of these phenomena it is possible to group together a number of facts whose association will lead to simplification of some morphological conceptions, and to other results of utility.

That the phenomena of Merism form a natural group is in some respects a familiar idea, but in its fullest expression it is as yet not

generally received, still less have the consequences which it entails been properly appreciated. Every one who has gone even a little way into morphological inquiry has met some of the difficulties to which we shall now refer.

It is with respect to the phenomena of Segmentation that these difficulties are most familiar, and it is in this connection that they may be best discussed. Segmentation is a condition which reaches its highest development in Vertebrates, the Annelids, and the Arthropods, and it is in these groups that it has been most studied. In them it appears as a more or less coincident Repetition of elements belonging to most of the chief systems of organs along an axis corresponding to the long axis of the body. To Segmentation of this kind the name "Metameric" has been given, and by many morphologists the attempt has been made, either tacitly or in words, to separate such Metameric Segmentation from other phenomena of Repetition elsewhere occurring. It has thus been attempted to distinguish the Repetitions which occur along the long axis of the body from those occurring along the long axis of appendages, such as for example the joints of antennæ or of digits, and some have even gone so far as to regard the Segmentation of the Vertebrate tail as a thing different in kind from that of the trunk itself. It would be apart from our present purpose to recur to these subjects, were it not that this suggestion of the existence of a difference in kind between Metameric Segmentation and other Repetitions has led to several notable errors in the interpretation of the facts of morphology and in the application of these facts to the solution of the problems of Descent. In order to lay a sound foundation for the study of Meristic Variation these errors must be cleared away, and to do this it is necessary to break down the artificial distinction between the phenomena of Metameric Segmentation and other cases of Repetition of Parts, so that the whole may be seen in their true relations to each other. When this is done, the mutual relations of the facts of Meristic Variation will also become more evident.

The first difficulty which has been brought into morphology by the suggestion that Metameric Segmentation is a phenomenon distinct in kind, is one which has coloured nearly all reasoning from the facts of Morphology to problems of phylogeny. For the existence of Metameric Segmentation in any given form is thus taken to be one of its chief characters, and, as such, is allowed predominant weight in considering the genetic relations of these forms. By the indis-

criminate though logical extension of this principle the conclusion has been reached that Vertebrates are immediately connected with, or have arisen by Descent from Annelids, or from Crustacea and the like, for the Repetition in these forms is closely similar. Others again, being struck with the resemblance between the Repetition of Parts along the radial axes of starfishes and those which occur along the long axes of Annelids, have hazarded the conjecture that perhaps this resemblance may indicate the actual phylogenetic history of these Repetitions. Though such speculations as these are little better than travesties of legitimate theory, some of them still command interest if not belief[1]. All alike are founded on the assumption that resemblances between the manner and degree in which Repetition occurs are unlikely to have arisen save by community of Descent. A broader view of Meristic phenomena will show that this assumption is unfounded; for so far are the expressions of it which are called Metamerism from standing alone, that it is almost impossible to look at any animal or vegetable form without meeting phenomena of Repetition which differ from Metamerism only in degree or in extent. Between these Repetitions and Metameric Repetitions it is impossible to draw any line, and the Meristic Variations of all will therefore be treated together.

The error in the estimate of the value of Metamerism as a guide to phylogeny is one by which the evidence of Variation is only indirectly affected. The other errors now to be mentioned are of a much more serious nature, for they concern the general conception of the nature of Homology which is the basis of all morphological study.

In introducing the method of the Study of Variation I have said that it can alone supply a solid foundation for inquiry into the manner by which one species arises from another. The facts of Variation must therefore be the test of phylogenetic possibility. Looking at organs instead of species, we shall now see that the facts of Variation must also be the test of the way in which organ arises from organ, and that thus Variation is the test of Homology. For the statement that an organ of one form is homologous with an organ of another means that

[1] These modern "Instances" recall many that once were famous but are now forgotten. For example: *Item non absurda est similitudo et conformitas illa, ut homo sit tanquam planta inversa. Nam radix nervorum et facultatum animalium est caput; partes autem seminales sunt infimæ, non computatis extremitatibus tibiarum et brachiorum. At in planta, radix (quæ instar capitis est) regulariter infimo loco collocatur; semina autem supremo.* Bacon, *Nov. Org.* Lib. II, 27. In *non computatis extremitatibus*, amateurs of INSTANTIÆ CONFORMES may still find matter for warning.

there is between the two some connection of Descent, and that the one organ has been formed by modification of the other, or both by modification of a third. The precise way in which this connection exists is not defined, and indeed has scarcely ever been considered, though such a consideration must sooner or later be attempted. We must for the present be content with the belief that in some undefined way there is a relationship between "homologous" parts, and that this is what we mean when we affirm that they are homologous.

We have however assumed that the transition from one form to another takes place by Variation. If therefore we can see the Variations we shall see the precise mode by which the descent is effected, and this must be true of the parts or organs as it is true of the whole body. In like manner then as the Study of Variation may be hoped to show the way by which one form passes into another, so also may it be hoped that it will show how the organs of one form take on the shape of the homologous organs of another.

In the absence of the evidence of Variation reasoning as to Homology rests solely on conjecture, and assumptions have thus been made respecting the nature of Homology which have coloured the whole of morphological study. Of these, two demand attention now.

I. *As to Homology between the Members of one Series.* We saw above (p. 250) how the resemblance between Repetitions occurring in divers forms has led to the belief that those forms had a common descent: in a somewhat similar way it has happened that the resemblance between individual members of a series of Repeated Parts has led to the belief that they must originally have been alike, and that they have been formed by differentiation of members originally similar. Many who would hesitate thus to formulate such a belief nevertheless have taken part in inquiries which can succeed only on the hypothesis that this has been the history of such parts. Of this nature are the old attempts to divide the skull into vertebræ, recognising the several parts of each; the modern disquisitions on the segmentation of the cranial nerves; the attempts to homologise the several phalanges of the vertebrate pollex and hallux with the several phalanges of the other digits; similar attempts to trace the precise equivalence of the elements of the carpus and tarsus, and many other quests of a like nature. In all these it is assumed that there is a precise equivalence to be found with enough searching, and that all the members of such series of Repetitions were originally alike. If the series of ancestors were before us it is expected that this would be seen to have been the case. In the light of the facts of Variation this assumption will be

seen to be a wrong one, and these simple views of the Repetition and Differentiation of members in Series must be given up as inadequate and misleading, even though there be no other to substitute.

II. *As to the individuality of Members of Series.* In seeking to homologise a Series of parts in one form with a Series of parts in another, cases often occur in which the whole Series of the one is admittedly homologous with the whole Series of the other. In such cases the question arises, can the principle of Homology be extended to the individual members of the two Series? If the two Series each contain the same number of members this question is a comparatively simple one, for it may be assumed that each member of the Series is the equivalent or Homologue of the member which in the other Series occupies the same ordinal position. If however the number of members differs in the two Series, how is the equivalence to be apportioned? This is a question again and again arising with regard to Meristic Series such as teeth, digits, phalanges, vertebræ, nerves, vessels, mammæ, colour-markings, the parts of the flower, and indeed in almost every system whether of animals or plants. To decide this question there are still no general principles. But though we yet know nothing as to the steps by which Meristic Variation proceeds, there is nevertheless a received view by which the interpretation of the phenomena is attempted, and though in the case of each system of organs the application of the principle is different, yet the principle applied is essentially the same.

Thus to compare the members of Series containing different members it is first assumed that the Series consisted ancestrally of some maximum number, from which the formula characteristic of each descendant has been derived by successive diminution. Here, again, I do not doubt that many who employ this assumption would hesitate to make it in set terms, but nevertheless it is the logical basis of all such calculations.

Now this hypothesis involves a definite conception of the mode in which Variation works, and it is most important that this should be realised clearly. For if it is true that each member of a Series has in every form an individual and proper history, it follows that if we had before us the whole line of ancestors from which the form has sprung, we should then be able to see the history of each member in the body of each of its progenitors. In such a Series the rise of an individual member and the decline of another should then be manifest. Each would have its individual history just as a Fellowship in a College

or a Canonry in a Cathedral has an individual history, being handed on from one holder to his successor, some being suppressed and others founded, but none merged into a common fund. In other words, according to the received view of the nature of these homologies, *it is assumed that in Variation the individuality of each member of a Meristic Series is respected.*

The difficulty in applying this principle is notorious, but when the evidence of Variation is before us the cause of the difficulty will become evident. For it will be found that though Variation may sometimes respect individual homologies, yet this is by no means a universal rule; and as a matter of fact in all cases of Meristic Series, as to the Variation of which any considerable body of evidence has been collected, numerous instances of Variation occur in which what may be called the stereotyped or traditional individuality of the members is superseded.

This error in the application of the principle of Homology to individual members of Meristic Series has arisen almost entirely through want of recognition of the unity of Meristic Repetition, wherever found. In the case of a series of parts among which there is no perceptible Differentiation, no one would propose to look for individual Homologies. For example, no one considers that the individual segments in the intestinal region of the earthworm have any fixed relations of this kind; no one has proposed to homologise single leaves of one tree with single leaves on another; it is not expected that the separate teeth of a roach have definite homologies with separate teeth of a dace, for such exceptions would be plainly absurd. But in series whose members are differentiated from each other the existence of such individuality is nevertheless assumed. To take only one case: a whole literature has been devoted to the attempt to determine some point in the vertebral column or in the spinal nerves from which the homologies of the segments may be reckoned. This is a problem which in its several forms has been widely studied. Some have attempted to solve it by starting from the lumbar plexus, while others have begun from the brachial. In the case of birds this question is reduced to an absurdity. Which vertebra of a pigeon, which has 15 cervical vertebræ, is homologous with the first dorsal of a swan which has 26 cervicals? To decide these questions the only possible appeal is to the facts of Variation, and judged by these facts the whole inquiry comes to an end, for it is seen at once that the expectation is founded on a wrong conception of the workings of Variation. No one,

as has been said above, would attempt such an inquiry if the Series were undifferentiated, for this individuality would not be expected in such a Series; but to suppose that it does exist in a differentiated Series of parts, is to suppose that with Differentiation the ordinal individuality of the members has become fixed beyond revision. This supposition the Study of Variation will dispel.

Here, as in the preceding case of the theoretical doctrine of Serial Homology, the current view is far too simple and far too human. Though the methods of Nature are simple too, yet their simplicity is rarely ours. In these subjective conceptions of Homology and of Variation, we have allowed ourselves to judge too much by human criterions of difficulty, and we have let ourselves fancy that Nature has produced the forms of Life from each other in the ways which we would have used, if we had been asked to do it. If a man were asked to make a wax model of the skeleton of one animal from a wax model of the skeleton of another, he would perhaps set about it by making small additions to and subtractions from its several parts; but the natural process differs in one great essential from this. For in Nature the body of one individual has never *been* the body of its parent, and is not formed by a plastic operation from it; but the new body is made again new from the beginning, just as if the wax model had gone back into the melting-pot before the new model was begun.

SECTION VII

Meristic Repetition and Division

Before ending this preliminary consideration of Merism it is right that we should see other aspects of the matter. What follows is put forward in no sense as theory or doctrine, but simply as suggesting a line of thought which should be in the minds of any who may care to pursue the subject further or to study the evidence. It is perhaps only when it is seen in connection with its possible developments that the magnitude of the subject can be fully felt.

In the treatises on Comparative Anatomy which belong especially to the beginning of this century, the idea constantly recurs that the series of segments of a metamerically segmented form do in some sort represent a series of individuals which have not detached themselves from each other. Seen in the light of the Doctrine of Descent this resemblance or analogy has been taken as a possible indication that

the segmented forms may actually have had some such phylogenetic history as this. By similar reasoning the Metazoa have been spoken of as "Colonies" of Protozoa. Now though we need not allow ourselves to be drawn away into these and other barren speculations as to phylogeny, we may still note the substance of fact which underlies them. For it is now recognised that between the process by which the body of a *Nais* is metamerically segmented, and that by which it divides into a chain of future "individuals," no line can be drawn: that the process of budding, or of strobilisation, by which one form gives rise to a number of detached individuals, is often indistinguishable from the process by which a near ally gives rise to a connected colony, and that the two processes may even be interchangeable in the same form; finally that the process of division of a fertilised ovum by the first cleavage plane may be in some essentials comparable with the division of a Protozoon into two new individuals. All these are now commonplaces of Natural History.

With what justice these considerations may have been applied to the problems of phylogeny we need not now inquire, but to the interpretation of the facts of Variation they have an application which ought not to be neglected.

If, then, as is admitted, there is a true analogy between the process by which new organisms may arise asexually by Division, and the process by which ordinary Meristic Series are produced, it follows that Variation, in the sense of difference between offspring and parent, should find an analogy in Differentiation between the members of a Meristic Series. Applied to the case of asexual reproduction there seems no good reason for denying this analogy. It is of course an undoubted fact that in the asexual reproduction of many forms Variation is rare, though the sexually produced offspring of the same forms are very variable. In plants this is familiar to everyone, though the extension of the same principle to animals rests chiefly on inference. Nevertheless in plants bud-variation, both Meristic and Substantive, happens often, and the division of a plant into two dissimilar branches may well be compared to the production of dissimilar offspring by one parent; indeed, if the processes of Division are admitted to be fundamentally the same, this conclusion can scarcely be escaped.

In one more aspect this subject may be considered with profit. It is, as we have seen, believed that the division of an ovum into two

segmentation-spheres is not a process essentially different from the division of certain Protozoa into two "individuals." In conceiving the manner of Variation in such Protozoa we have little or no fact to guide us, but this much is obvious: that for the introduction of a variety as the offspring of a given species, it is necessary either that the two parts into which the unicellular organism divided should have varied equally, and that the division should thus be a symmetrical division (in the full sense of qualitative as well as formal symmetry); or that the division should be asymmetrical, the resulting parts being dissimilar, in which case one may conceivably belong to the type and the other be a Variety. If Variation has ever occurred in the reproduction of animals of this class it must have occurred on one or both of these plans.

Returning to the segmentation of the Metazoan ovum we have the well-known results of Roux and others, showing that, in certain species, the first[1] cleavage-plane divides the body into the future right and left halves. In such cases then on the analogy of the Protozoon, the right and left halves of the body are in a sense comparable with the two young Protozoa, and though each half is hemi-symmetrical, it is in this way the equivalent of a separate organism. This suggestion, which is an old one, receives support from many facts of Meristic Variation, especially from the mode of formation of homologous Twins and "double Monsters" which are now shown almost beyond doubt to arise from the division of one ovum[2]. But besides the evidence that each half of the body may on occasion develop into a whole, evidence will be given that one half may vary in its entirety, independently of the other half. Such Variation may be one of sex, taking the form of Gynandromorphy, so well known among Lepidoptera, in which the secondary sexual characters of one side are male, those of the other being female; or it may happen that the difference between the two sides is one of size, the limbs and

[1] Often it is the second cleavage-plane (if any) which corresponds with the future middle line.

[2] The well-known evidence relating to this subject will be spoken of later. The view given above, which is now very generally received, finds support in the striking observations of Driesch, lately published (*Zt. f. w. Zool.* 1891, LIII, p. 160). Working with eggs of *Echinus*, Driesch found that if the first two segmentation-spheres were artificially separated, each grew into a separate *Pluteus*; if the separation was incomplete, the result was a double-monster, united by homologous surfaces. Similar experiments attended by similar results have since been made on *Amphioxus* by E. B. Wilson, *Anat. Anz.* VII, 1892, p. 732.

organs of one side being smaller than those of the other; or lastly the Variation between the two sides may be one that has been held characteristic of type and variety or even of so-called species and species[1].

These matters have been alluded to here as things which a student of the facts of Variation will do well to bear in mind. It is difficult to see the facts thus grouped without feeling the possibility that the resemblance between the two sides of a bilaterally symmetrical body may be in some essentials the same as the resemblance between offspring of the same parent, or to use an inclusive expression, that the resemblance between the members of a Meristic Series may be essentially the same as the resemblance and relationship between the members of one family; that the members of a row of teeth in the jaw, of a row of peas in a pod, of a chain of salps, or even a litter of pigs, all resulting alike from the processes of Division, may stand to each other in relationships which though different in degree may be the same in kind.

If reason shall appear hereafter for holding any such view as this, the result to the Study of Biology will be profound. For if it shall ever be possible to solve the problem of Symmetry, which may well be a mechanical one, we shall thus have laid a sure foundation from which to attack the higher problem of Variation, and the road through the mystery of Species may thus be found in the facts of Symmetry.

SECTION VIII

Discontinuity in Substantive Variation: Size

From this subject of Merism and the thoughts which it suggests, we now pass to another matter. The first limitation by which we proposed to group Variations was found in the characters which they affect: the second relates to the magnitude, or as I shall call it, the **Continuity** of the Variations themselves. And though for many, a conception has no value till it be cast in some finite mould, my aim will be rather to describe than to define the meaning of the term Continuity as applied to Variation. In dealing with a subject of this obscurity, where the outlines are doubtful, an exact mapping of the facts cannot be made and ought not to be attempted; but I trust that

[1] Evidence of such abrupt Variation between the two sides of the body belongs for the most part to the Substantive group.

from the present indications, vague though they are, some larger and more definite conception of Discontinuity in Variation may shape itself hereafter by a process of natural growth. For this reason I shall as far as possible avail myself of examples rather than of general expressions, whether inclusive or exclusive.

To those who have studied the recent works of Galton, the conceptions here outlined will be familiar. In the chapter on "Organic Stability" in *Natural Inheritance*, the matter has been set forth with charming lucidity, and what follows will serve chiefly to illustrate the manner in which the facts of Natural History correspond with the suggestions there made.

In the case of most species it is a matter of common knowledge that though no two individuals are identical, there are many which in the aggregate of their characters nearly approach each other, constituting thus a normal, from which comparatively few differ widely. In such a species the magnitude of these differences is proportional to the rarity of their occurrence. Now this, which is a matter of common experience, has been shown by Galton to be actually true of several quantities which in the case of Man are capable of arithmetical estimation. In the cases referred to it has thus been established that these quantities when marshalled in order give rise to a curve which is a normal curve of Frequency of Error. Taking for instance the case of stature, Galton's statistics show that for a given community there is a mean stature, and the distribution of the statures of that community around the mean gives rise to a Curve of Error. In this case the individuals of that community in respect of stature form one group. Now in the case of a collection of individuals which can be separated into two species, there is some character in respect of which, when arranged by the statistical method, the individuals do not make one group but two groups, and the distribution of each group in respect of that character cannot be arranged in one Curve of Error, though it may give rise to two such curves, each having its respective mean. For example, if in a community tall individuals were common and short individuals were common, but persons of medium height were rare, the measurements of the stature of such a community when arranged in the graphic method would not form one Curve of Error, though they might and probably would form two. There would thus be a normal for the tall breed, and a normal for the short breed. Such a community would, in respect of stature, be what is called *dimorphic*. The other case, in which the whole community,

grouped according to the degrees in which they display a given character, forms one Curve of Error, may conveniently be called *monomorphic* in respect of that character. By considering the possible ways in which such a condition of dimorphism may arise in a monomorphic community, one of the uses of the term Discontinuity as applied to Variation will be made clear.

Considering therefore some one character alone, in a species which is monomorphic in respect to that character, individuals possessing it in its mean form are common while the extremes are rare; while if the species is dimorphic the extremes are common and the mean is rare. Now the change from the monomorphic condition to the dimorphic may have been effected with various degrees of rapidity: for the frequency of the occurrence of the mean form may have gradually diminished, while that of the extremes gradually increased, through the agency of Natural Selection or otherwise, in a long series of generations; or on the other hand the diminution in the relative numbers of the mean individuals may have been rapid and have been brought about in a few generations by a few large and decisive changes, whether of environment or of organism.

Referring to the curve of Distribution formed in the graphic method of displaying the statistics, during the monomorphic period the curve has one apex corresponding with the greatest frequency of one normal form, but in the dimorphic period the curve has two apices, corresponding with the comparative frequency of the two extremes, and the comparative rarity of the mean form. The terms Continuous or Discontinuous are applicable to the process of transition from the monomorphic to the dimorphic state according as the steps by which this change was effected are small or large.

The further meanings of Discontinuous Variation will be explained by the help of examples. The first cases refer to Substantive Variation[1], and we may conveniently begin by examining a case of Variation in a character which is easily measured arithmetically.

Among beetles belonging to the Lamellicorn family there are numerous genera in which the males may have long horns arising

[1] In referring thus to evidence as to Substantive Variation, I find myself in the difficulty mentioned in the Preface. For it is necessary to allude to matters which cannot be properly treated in this first instalment of facts. In order, however, that the one introductory account may serve for all the evidence together, such allusion is inevitable and I can only trust that full evidence as to Substantive Variation may be produced before long.

from various parts of the head and thorax[1]. These horns may be of very great size, as in the well-known Hercules beetle (*Dynastes hercules*) and others. The females of these forms are usually without horns. In such genera it is commonly found that the males are not all alike, but some are of about the size of the females and have little or no development of horns, while others are more than twice the size of the females and have enormous horns. These two forms of male are called "low" and "high" males respectively.

In many places in the Tropics such beetles abound, both "high" and "low" males occurring in the same locality. An admirable

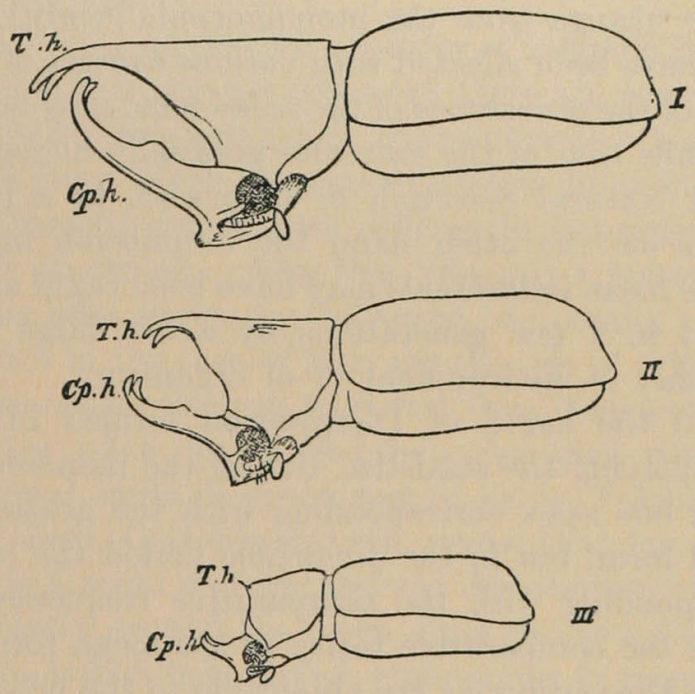


Fig. 1. Side-views of the Lamellicorn beetle, *Xylotrupes gideon*. Legs not represented. I, High male; II, Medium male; III, Low male.

example of this phenomenon is seen in *Xylotrupes gideon*, of which a "high," "low," and medium male are shown in profile in Fig. 1. Of this insect a very large number were kindly given to me by Baron Anatole von Hügel, who collected them at one time, in one locality, in Java. In this species there is one cephalic and one thoracic horn, placed in the positions shown in the figure. Fig. 1, I shows a "high" male, II is a medium, and III a "low" male. In the gathering received there were 342 males. My friend, Mr H. H. Brindley, has made careful measurements of the lengths of the horns of these specimens

[1] For particulars of this subject with illustrations, see *Descent of Man*, 1st ed., vol. I, pp. 369–372. A detailed account of this and the succeeding example in the case of the earwig was given by Mr Brindley and myself in *P.Z.S.* 1892 [p. 197 *supra*. Ed.].

and has constructed the diagram, Fig. 2. In this each dot represents an individual, and the abscissæ show the measurements of the length of the cephalic horn. For clearness these measurements are represented as four times the natural size. So far as the numbers go the result shows that the most frequent forms are the moderately low and the moderately high, the forms of mean measurement being comparatively scarce. It is true that the numbers are few, but so little heed is paid to phenomena of this kind that material is difficult to obtain and the present opportunity was indeed wholly exceptional[1].

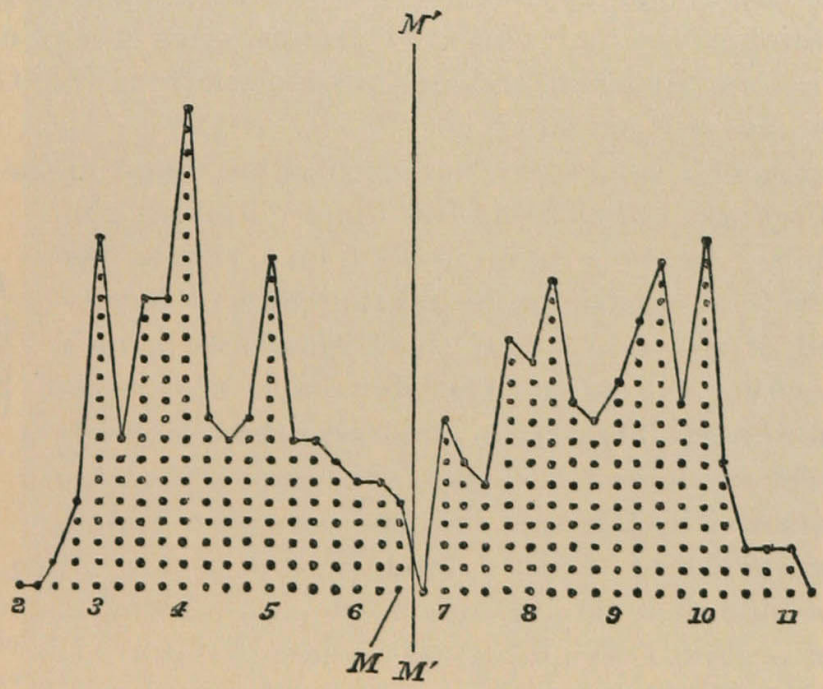


Fig. 2. Diagram representing the frequency of the lengths of cephalic horn in male *Xylotrupes gideon*. *M*, the mean case; *M'* the mean value. The abscissæ give lengths of cephalic horn in lines.

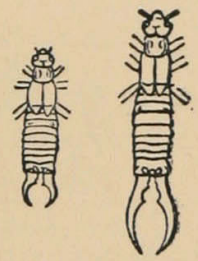
But taking the evidence for what it is worth, the comparative scarcity of "medium" males in that particular sample is clear, and so far the form is dimorphic and has two male normals.

Now such a condition may have arisen in several ways. First, in the past history of the species there may have been a time when the males were horned and were monomorphic, the "medium" form being the most frequent, and the present dimorphic condition may have

[1] In the Lucanidæ, of which the Stagbeetle (*L. cervus*) is an example, a similar phenomenon occurs, the "high" and "low" males being distinguished by the degree of development of the mandibles. No sufficient number of male Stagbeetles has yet been received to warrant any statement as to the frequency of the various types of males.

been derived from this, either continuously or discontinuously as described above for the case of Stature. Secondly, the dimorphism may date from the first acquisition of the horns, and this character may perhaps have always been distributed in the dimorphic way. In this case the term Discontinuous would be applicable to the Variation by which the groups of "high" and "low" males have been severally produced. I am not acquainted with evidence as to the course of inheritance in these cases, and I do not know therefore whether both "high" and "low" males may be produced by one mother. If this should be shown to be the case, it would suggest that the separation of the males into two groups was a case of characters which do not readily blend, and are thus exempt from what Galton has called the Law of Regression[1].

In the case of a somewhat similar structure found in the common earwig (*Forficula auricularia*) the dimorphism is still more definite. In the autumn of 1892 on a visit to the Farne Islands, a basaltic group off the coast of Northumberland, it was found that these islands teem with vast quantities of earwigs. The abundance of earwigs was extraordinary. They lay in almost continuous sheets under every stone and tussock, both among the sea-birds' nests and by the light-keepers' cottages. Among them were males of the two kinds shown in Fig. 3; the one or high male having forceps of unusual length, the other or low male, being the common form. It appears that the high male is known from many places in England and elsewhere and that it was made into a distinct species, *F. forcipata*, by Stephens[2] though by later authorities[3] the species has not been retained. A large sample of earwigs collected in a Cambridge garden contained 163 males of which five would come into the high class, but the great abundance of high males at the Farnes seems to be quite exceptional.



I. II.

Fig. 3. I, Low male, II, High male of common earwig (*Forficula auricularia*) from the Farne Islands.

With a view to a statistical determination of the frequency of the high and low forms 1000 of these earwigs were collected by Miss A. Bateson, the whole being taken at random on one day from three very small islands joined to each other at low tide. Of the 1000

[1] *Natural Inheritance*, pp. 88–110.

[2] Stephens, *Brit. Ent.* 1835, VI, p. 6, Pl. XXVIII, fig. 4.

[3] Fischer, *Orthop. Europ.* 1853, p. 74; Brunner von Wattenwyl, *Prodr. d. europ. Orthop.* 1882, p. 12.

specimens 583 proved to be mature males with elytra fully developed, no specimen with imperfect elytra being included in this number[1]. On measuring the length of the forceps to the nearest half mm. and grouping the results in the graphic method the curve shown in Fig. 4 was produced. The figures on the ordinates here show the numbers of individuals, those on the abscissæ giving the length of the forceps in millimetres. As there shown the smallest length of forceps was 2·5 mm. and the greatest 9 mm., the greatest frequency being grouped

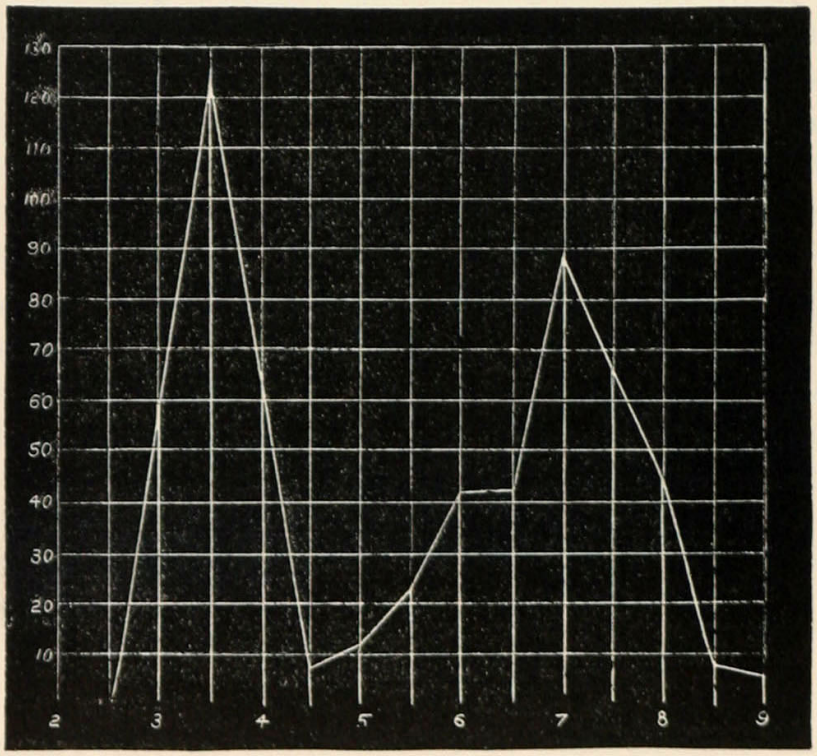


Fig. 4. Curve showing frequency of various lengths of forceps of male earwigs (*F. auricularia*) from the Farne Islands. Ordinates, numbers of individuals: abscissæ, lengths of forceps in mm.

about 3·5 mm. and 7 mm. respectively. The mean form having forceps of moderate length is comparatively rare. The size of the forceps of the females scarcely varies at all, probably less than 1 mm. in the whole sample.

The number of cases is enough to fairly justify the acceptance of these statistics and it is not likely that a greater number of cases would much alter the shape of the curve. Here, therefore, is a group of individuals living in close communion with each other, high and low, under the same stones. No external circumstance can be seen

[1] For particulars in evidence of the maturity of these specimens see *P.Z.S.* 1892 [p. 195 *supra*. Ed.].

to divide them, yet they are found to consist of two well-marked groups.

Before leaving these examples special attention should be directed to the fact that the existence of a complete series of individuals, having every shade of development between the "lowest" and the "highest" male, does not in any way touch the fact that the Variation may be Discontinuous; for we are concerned not with the question whether or no all intermediate gradations are possible or have ever existed, but with the wholly different question whether or no the normal form has passed through each of these intermediate conditions. To employ the metaphor which Galton has used so well—and which may prove hereafter to be more than a metaphor—we are concerned with the question of the positions of Organic Stability; and in so far as the intermediate forms are not or have not been positions of Organic Stability, in so far is the Variation discontinuous. Supposing, then, that the "high" and "low" males should become segregated into two species—a highly improbable contingency—these two species would have arisen by Variation which is continuous or discontinuous according to the answer which this question may receive.

SECTION IX

Discontinuity in Substantive Variation: Colour and Colour-Patterns

From the consideration of Discontinuity in the Variation of a character, size, which may be readily measured arithmetically, we pass to the more complex subject of Discontinuous Variation in qualities which are not at once capable of quantitative estimation. In this connection the case of Colour-variation may be profitably considered. Nature abounds with examples of colour-polymorphism, and in numerous instances such Variation is discontinuous. Of such discontinuous Variation in colour I shall speak under two heads, considering first variations in colours themselves and secondly variations in colour-patterns. As it is not proposed to give the evidence as to Substantive Variation in this volume, a few examples must suffice to show the use of the term Discontinuity as applied to these Colour-variations.

I. *Colours.* The case of the eye-colour of Man may well be mentioned first, as it has been studied statistically by Galton. In this

case the facts clearly showed that certain types of eye-colour are relatively common and that intermediates between these types are comparatively rare. The statistics further showed that in this respect inheritance was alternative, and that the different types of eye-colour do not often blend in the offspring. "If one parent has a light eye-colour and the other a dark eye-colour, some of the children will, as a rule, be light and the rest dark; they will seldom be medium eye-coloured, like the children of medium eye-coloured parents[1]."

Colour dimorphism of this kind is very common among animals and plants. It is well known, for example, among beetles. Several metallic blue beetles have bronze varieties of both sexes, living together in the same locality. A familiar instance of this dimorphism occurs in the common *Phratora vitellinæ*. Again in the Elaterid beetle, *Corymbites cupreus*, there is a similar dimorphism in both sexes, the one variety having elytra in larger part yellow-brown, while the elytra of the other are metallic blue. This blue variety was formerly reckoned a distinct species, *C. æruginosus*. In the latter case I am informed by Dr Sharp, who has had a large experience of this species, that no intermediate between these two varieties has been recorded, and in the case of the *Phratora* the occurrence of intermediates is very doubtful. Another common example of colour dimorphism is seen in *Telephorus lividus*, the "sailor" of "soldiers and sailors." This beetle may be found in large numbers, about half being slaty in colour (var. *dispar*), while the remainder have the yellowish colour which coleopterists call "testaceous." Such instances may be multiplied indefinitely. When the whole evidence is examined it will be found that different colours are liable to different discontinuous variations; as instances may be mentioned black and tan in dogs; olive-brown or green and yellow in birds, etc.[2]; grey and cream-

[1] *Natural Inheritance*, p. 139.

[2] A specimen of the green ring parakeet (*Palæornis torquatus*) at the Zoological Society's Gardens was almost entirely canary-yellow in 1890. Since that date it has become more and more "ticked" with green feathers. A green woodpecker (*Picus viridis*) is described, having the feathers of the rump edged with red instead of yellow, the normally green feathers of the three lower rows of wing-covers and the back were pointed with yellow. J. H. Gurney, *Zoologist*, XI, p. 3800. I am indebted to Mr Gurney for the loan of a coloured drawing of this specimen. Another example is described as being entirely canary-yellow, with the exception of a few feathers on the cap, which were purple-red. De Betta, *Mater. per una fauna Veronese*, p. 174. For this reference I am indebted to Prof. Newton. Specimen of common bunting whitish yellow. Edward, *Zool.* 6492; sedge warbler canary-yellow. Bird, *Zool.* 3632. The canary itself is a similar case. An eel gamboge-yellow. Gurney, *Zool.* 3599.

colour in mice and cygnets[1]; red and blue in the eggs of many Copepoda[2], the tibiæ of locusts[3], the hind-wings of the crimson underwing (*Catocala nupta*)[4], etc. Another case of blue as a variety of scarlet is the familiar one of the flower of the pimpernel (*Anagallis arvensis*). Discontinuous colour-variation of this kind is one of the commonest phenomena in nature, but to advance the subject materially it is necessary for a large mass of evidence to be produced. This cannot now be attempted, but in order to bring out the close relation between these facts and the problem of Species I propose to dwell rather longer on one special section of the evidence which must serve to exemplify the rest. The case which I propose to take is that of certain yellow, orange, and red pigments. For brevity I shall present the chief facts in the first instance without comment.

1. *Colias edusa* (Clouded Yellow) is usually orange-yellow, having a definite pale yellow female variety, *helice*, which is not recognised as occurring in the male form. A specimen is figured having the right side

[1] In this case I can affirm the alternative character of the inheritance. For several years a pair of swans kept by St John's College, Cambridge, have produced cygnets, some of which have been of the normal grey, while others have been fawn-colour, a condition which Prof. Newton tells me has been thought characteristic of the "Polish" swan, a putative species. None of these cygnets are intermediate in colour, and all acquire the full white adult plumage, but the feet of the fawn-coloured cygnets remain pale in colour. Now the father of these has pale feet and was doubtless himself a fawn-coloured cygnet; the hen is normal. The cock formerly belonged to Dr Gifford, who kindly told me that the cygnets of this bird by a different hen were also thus diverse. A pair of these were given to Sir John Gibbons, who informs me that "from these there has been a brood every year, and always I think *one* of the cygnets has been white or nearly so, the others being of the usual colour." One of Dr Gifford's birds was also given to the late Mrs Gosselin of Blakesware, to whom I am indebted for descriptions of and feathers from several fawn-coloured cygnets which were its offspring. A similar case on the Lake of Geneva is recorded by Fauvel, *Rev. Zool.* 1869, p. 334, and another in the Zoological Gardens at Amsterdam, by Newton, *Zool. Rec.* 1869, p. 99.

[2] This is well known to collectors of fresh-water fauna, and I have repeatedly seen the same phenomenon in species of *Diaptomus*, especially *D. asiaticus*, in the lakes of W. Siberia. Among thousands of individuals with red-brown egg-sacs will often occur a few specimens having the egg-sacs of a brilliant turquoise-blue. In this connection compare the case of the crayfish (*Astacus fluviatilis*), which turns scarlet on being boiled, and which, like the lobster, not uncommonly appears in a full blue variety.

[3] *Caloptenus spretus* with hind tibiæ blue instead of red, Dodge, *Can. Ent.* 1878, x, p. 105; *Melanoplus packardii*, having hind tibiæ red instead of bluish, Bruner, *Can. Ent.* 1885, xvii, p. 18. For reference to these observations I am indebted to Cockerell, *Ent.* 1889, xxii, p. 127.

[4] White, *Ent.* 1889, xxii, p. 51. Compare the fact that in another species of *Catocala* (*C. fraxini*), the Clifden Nonpareil, the hind-wings are normally bluish.

helice and the left *edusa*. Fitch, E. A., *Entomologist*, 1878, XLI, p. 52, Pl. fig. 11. This was an authentic specimen, for Mr Fitch tells me that it was taken by his son and seen alive by himself.

A specimen having one wing white and the rest orange is recorded by Morris, *Brit. But.* p. 13.

Intermediates between *edusa* and *helice* must be exceedingly rare. Oberthür records two such specimens and says that Staudinger took a similar one at Cadiz. For this intermediate he proposes a new name, *helicina*. *Bull. Soc. Ent. Fr.* (5), x, p. cxlv.

A curious specimen, apparently a *male*, having the colour of *helice* was kindly shown me by Mr F. H. Waterhouse. The light marks which in the female are present on the dark borders of the fore-wing are only represented by one minute light mark on each fore-wing.

In most if not all of the *edusa* group of *Colias*, there is a pale aberration of the female, corresponding to the *helice* variety of *edusa*. Elwes, *Tr. Ent. Soc.* 1880, p. 134. In the same paper is a full account of the geographical distribution of the several species and colour-varieties of *Colias*.

Colias hyale (Pale Clouded Yellow) is normally sulphur-coloured. Nearly white varieties and a variety with the field rich sulphur colour, and the apical marginal patches red, are recorded in several works.

2. *Gonepteryx rhamni* (the Brimstone) is sulphur-yellow in the male, and greenish-white in the female. There is a spot in each wing, and the scales covering this on the upper side are bright orange.

Gonepteryx cleopatra, a S. European species, is like the above in the hind-wings, while the field of the fore-wings is flushed with orange of exactly the tint of that on the spots of *G. rhamni*.

There are several records in entomological literature alleging the capture of "*G. cleopatra*" in Britain, *e.g. Proc. Ent. Soc.* 1887, p. xliii.

In addition to these there are records of specimens of *G. rhamni* more or less flushed with orange; *e.g.* a specimen at Aldershot with orange spots on fore-wings as in *cleopatra*, *Proc. Ent. Soc.* 1885, p. xxiv. Mr Jenner Weir said he had seen a specimen in Ingall's collection, intermediate between *rhamni* and *cleopatra*. *Ibid.*

A male of *G. rhamni* taken at Beckenham had the costal margin of each fore-wing broadly but unequally suffused with bright rose-colour or scarlet, and the right posterior wing was marked in like manner. The insect was thus marked when captured. Bicknell, *Proc. Ent. Soc.* 1871, p. xviii.

3. *Anthocharis* (*Euchloe*) *cardamines* (the Orange Tip) in the male has the fore-wings tipped with orange on both sides, while in the female these orange tips are absent. The field in both is white. In entomological literature are many records of variations in the extent and depth of the orange

markings on upper or under side, or both (cp. *Zoologist*, XIII, 4562; *Proc. Ent. Soc.* 1870, p. ii; Mosley, *Illustrations of British Lepidoptera*; Haworth; Boisduval and many others), but with these we are not immediately concerned.

A specimen is figured in which the orange spots were completely represented by yellow. Mosley, *Illustrat. Brit. Lep.*

The white of the field is replaced by primrose or lemon yellow in several Continental forms. These have been described as species under the names *eupheno*, *belia*, *euphenoides*, *gruneri*, etc.

A local variety of *A. eupheno* is described from Mogador, where it was found common at a little distance from the town. The female was much larger than the type, resembling the male in markings and in shape of the fore-wings. The orange blotch, instead of being confined to tip of the fore-wing as normally, extends to the discoidal spot and is usually bounded by a black band, sometimes suffusing the whole tip of the wing. The colour of the field varies from pure white to pale lemon: the hind-wings are always yellower than in the type, in some specimens being nearly as yellow as those of the male. Mr M. C. Oberthür supplied a specimen from Central Algeria which was intermediate between the type and this variety. Leech, J. H., *P.Z.S.* 1886, p. 122.

4. Amongst Lepidoptera the change from red to yellow is very common. A case of *Vanessa atalanta*, having the red partially replaced by yellow, is figured in *Entom.* 1878, XI, p. 170, Pl. Varieties of *Arctia caja*, *Callimorpha dominula*, *C. hebe*, *C. hera*, *C. jacoboeæ*, *Zygœna filipendulæ*, *Z. minos*, etc., with yellow instead of red, are to be seen in many collections. See especially Ochsenheimer, *Schm. v. Europa*, 1808, II, p. x, also p. 25, and many other authors. A chalk-pit at Madingley, Cambridge, has long been known to collectors as a locality for the yellow *Z. filipendulæ* (Six-spot-Burnet); see *Ent. Mo. Mag.* XXV, p. 289. In some of these the yellow is tinged with red, but it is commonly a very distinct variety. A variety of the red underwing (*Catocala nupta*) with brownish-yellow in the place of the red, is figured by Engramelle, *Papill. d'Eur.*, Pl. CCCXXII. The evidence relating to this subject is very extensive, and concerns many genera and species besides those named above.

5. *Pericrocotus flammeus* (an Indian fly-catcher) is grey and yellow in the female, and black and orange-red in the male. The young male is grey and yellow like the female. An adult male is described in which the grey had been fully replaced by black, but the yellow remained, not having been replaced by red. R. G. Wardlaw Ramsay, *P.Z.S.* 1879, p. 765. See also Legge, *Birds of Ceylon*, I, p. 363, for description of male in transitional plumage.

Curiously enough the change from red to yellow and from light yellow to dark is no less common among plants, though it can scarcely be supposed that the substances concerned are similar.

1. *Narcissus corbularia* and other species are known in sulphur-yellow and in full yellow[1].

2. The Iceland poppy (*P. nudicaule*) is very common in gardens under three forms, white, yellow and orange. Intermediate and flaked varieties occur, but are less common than the three chief forms. Respecting this species Miss Jekyll of Munstead, who first brought out the varieties, kindly gives me the following information. She writes: "I began with one plant of the yellow colour that I take to be the type-colour. It was then new as a garden plant, so I saved the seed. The first sowing gave me various shades of orange, as well as the type, in different shades. In the 3rd and 4th years I got buffs, whites, and very pale lemon colourings. As there was only one plant to begin with there was no question of cross-fertilisation. A white appeared in the 3rd year of sowing and I kept on selecting for 2 or 3 years ...and gave it to a friend in Ireland, who returned it to me 2 years later still more improved. This strong white seems now to be fixed and quite unwilling to revert to the yellow colourings, and is a rather stouter and handsomer plant altogether." In seedlings from the orange or yellow form grown in separate beds the proportion of seedlings true to their parent colour would not be nearer than about 60 or 70 per cent., but in the case of the white form Miss Jekyll considers that 95 per cent. may be expected to come true.

The yellow horned poppy (*Glaucium luteum*) is normally of a lemon yellow very like that of *P. nudicaule*. Of this species also there is an orange cultivated variety. The varieties of the tomato offer a similar series of colour-variations.

3. Fruits of many kinds are known in red and yellow forms. For instance the yellow berried yew is well known. It is described under the name *Taxus baccata fructu-luteo*, Loud. "It appears to have been discovered about 1817 by Mr Whitlaw of Dublin, growing in the demesne of the Bishop of Kildare, near Glasnevin; but it appears to have been neglected till 1833 when Miss Blackwood discovered a tree of it in Clontarf churchyard near Dublin. Mr Mackay on looking for this tree in 1837 found no tree in the churchyard, but several in the grounds of Clontarf Castle, and one, a large one, with its branches overhanging the churchyard, from which he sent us specimens. The tree does not differ, either in its shape or

[1] Mr P. Barr, who has collected these forms in Portugal, tells me that he believes the pale ("*citrina*") varieties of *N. ajax* and *N. corbularia* to be confined to calcareous soils.

foliage, from the common yew, but when covered with its berries it forms a very beautiful object, especially when contrasted with yew trees covered with berries of the usual coral colour." Loudon, *Arb. et Frut. Brit.* IV, 1838, p. 2068.

4. The raspberry (*Rubus idæus*) is another fruit which is known wild in both the red and yellow forms, though the latter is less common. According to Babington, it has pale prickles, and leaflets rather obovate. *Brit. Rubi*, p. 43. (See Rivers, *Gard. Chron.* 1867, p. 516.)

Any person who has opportunities of handling animals and plants in numbers can add many similar cases. These few are taken more or less at random, as illustrations of the frequency with which red, orange and yellow may vary to each other. It is of course not necessary to say that in numerous instances both among animals and plants, the same parts which in one species are yellow, in an allied species or in a geographically distinct race are represented by orange or by red. To an appreciation of the rapidity with which such changes may have come about, facts like the foregoing contribute.

The frequency of such variations suggests that many of these yellow and red pigments are either closely allied bodies or different forms of the same body. Until the chemistry of these substances has been properly investigated nothing can be definitely stated as to this, but the fact that vegetable yellows are very sensitive to reagents is familiar. The lemon variety of the Iceland Poppy treated with ammonia turns to a colour almost identical with that of the orange variety, while the white variety so treated goes primrose yellow. The lemon variety when boiled or treated with alcohol yields an orange solution, which is of the same tint. This returns to lemon-colour if treated with ammonia or acids. The wings of *G. rhamni* when boiled yield a soluble yellow, which according to Hopkins (*Proc. Chem. Soc.* reported *Nature*, Dec. 31, 1891) is a derivative of mycomelic acid, allied to uric acid. This substance turns orange with reagents. The wings of *G. rhamni* turn orange-red when exposed to wet potassium cyanide (*Proc. Ent. Soc.* 1871, p. xviii), as may be easily seen.

When these facts, meagre though they are, are considered together with the evidence of variability, the suggestion is very strong that the discontinuity between these several characteristic colours is of a chemical nature, and that the transitions from one shade of yellow to another, or from yellow to orange or red is a phenomenon comparable with the changes of litmus and some other vegetable blues from blue to red or of turmeric from yellow to brown. If such a view

of these phenomena were to be accepted, it would, I think, be simpler to regard the constancy of the tints of the several species and the rarity of the intermediate varieties as a direct manifestation of the chemical stability or instability of the colouring matters, rather than as the consequences of environmental Selection for some special fitness as to whose nature we can make no guess. For we do know the phenomenon of chemical discontinuity, whatever may be its ultimate causes, but of these hypothetical fitnesses we know nothing, not even whether they exist or no.

II. *Colour-patterns.* Thus far I have spoken only of discontinuous Variations in colours themselves, but there are no less remarkable instances of discontinuous Variations in the distribution of colours in particoloured forms. By a combination of these modes, Variations of great magnitude may occur.

One of the most obvious cases of this phenomenon is that of the cat. In European towns cats are of many colours, but they nevertheless fall very readily into certain classes. The chief of these are black, tabby, silver-grey and silver-brindled, sandy, tortoiseshell, black and white, and white. Of course no two cats have identical colouring, but the individual Variations group very easily round these centres, and intermediate forms which cannot at once be referred to any of these groups are immediately recognised as something out of the common and strange. Yet it is almost certain that cats of all shades breed freely together, and there is no reason to suppose that the discontinuity between the colour-groups is in any way determined by Natural Selection.

Another example may be seen in the dog-whelk (*Purpura lapillus*). This animal occurs on nearly the whole British coast, wherever there are rocks or even clay hard enough to form definite crevices. Like most littoral animals, the dog-whelks of each locality differ more or less from those of other localities, and these differences may be differences of size, texture of shell, degree of calcification, amount of "frilling," etc. The peculiarities may be so striking that each individual can at once be recognised as belonging to a given locality, or they may be trifling, and appreciable only when a large number of individuals are gathered. But apart from these differences of form and texture there are a great number of colour-varieties of which the following are the three chief whole-coloured forms, viz. white, dark purple-brown, and yellow. In addition to these there are banded

forms, and the bands may be coloured with any two of the three colours mentioned above. Among the banded forms there are two distinct sorts of banding, in the one there are very many fine bands and in the other there are a few broad bands. In most localities these colour-varieties may all be found; though in some places, especially where the water is foul, as at Plymouth, the shells are greatly corroded and the colours, if originally present, are obscured. Speaking however of localities in which colour-varieties are to be seen at all, several may generally be found together. If any one will take the trouble to gather a few hundreds of these shells and will set himself to sort them into groups according to their colours, he will find that the majority fall naturally into groups of this kind; and that those which cannot be at once assigned to groups but fall intermediately between the groups are comparatively few. I have seen this at many places on the English coast; in Yorkshire, Norfolk, Suffolk, Kent, Sussex, Dorsetshire, Devonshire, Cornwall, etc. In several localities I have found pairs belonging to different colour-varieties breeding together, and there is therefore no reasonable doubt that these colour-variations do not freely blend, but are discontinuous.

The statements here made with regard to *P. lapillus* hold in almost the same way for *Littorina rudis*, but in this case the number of colour-types is larger. In *L. rudis* I have occasionally seen specimens of which the upper part belonged to one colour-type, and the lower to another, the transition occurring sharply at one of the varices. In these cases the shell appears to have been injured and is possibly renewed.

One of the commonest British lady-birds (*Coccinella decem-punctata*) is an extremely variable form. A great number of its varieties may be found together, ranging from forms with small black spots on a red field to forms in which the field is black with a few red spots. But in spite of the great diversity there are certain types which are again and again approached, while the intermediates are comparatively scarce.

The following case, well known to entomologists, may be mentioned here. The Painted Lady (*Pyrameis cardui*) is found in the typical form over the entire extent of every continent, with the exception of the Arctic regions and possibly S. America. A special form of it (var. *kershawi*) is found in Australia and New Zealand, but the other large islands south of Asia possess the normal type. The latter is also found in the Azores, Canaries, Madeira and St Helena. This butterfly has been taken on the snow-level

in the Alps; and in N. America, though it may be regarded as one of the commonest butterflies in the elevated central district, it is most abundant at a level of 7000–8000 feet. It has been taken on Arapahoe Peak, between 11,000 and 12,000 feet (from Scudder, *Butterflies of N. America*, I, pp. 477–480). Of this insect, which is a very constant one, a certain striking aberration has been found, always as a great rarity, in many lands. In this aberration the markings are almost entirely rearranged. It is said to have been first described by Rambur under the name var. *Elymi*, but this description I have never found. (The reference quoted is *Annales des Sci. d'Observation*, Paris, 1829, vol. II, Pl. v.) As often happens with Variation, without coloured figures description is almost useless, but the figures referred to are very accessible. In a British specimen of this aberration the white bars are absent from the anterior costæ and a series of white fusiform blotches are present along the marginal border; two abnormal white spots are also present near the anal angle, thus continuing the series down the wing (Fig. 5, A). The hind-wings are equally aberrant. The two large spots which are usually on the disk between the median nervure and the inner margin are altogether wanting. Between each of the nervures of the hind-wing is a white spot, whereas in the normal form there is no white spot at all on the hind-wings. These white spots on the hind-wings form a row parallel to the border of the wing and, as it were, continue the series of white spots borne by the anterior wings. [Underside not described.] This specimen was reared from a larva found near the river Lea, Clapton Park. Clark, J. A., *Entomologist*, 1880, XIII, p. 73, fig. A coloured figure of the same specimen, Mosley, S. L., Pl. 8, fig. 3.

A form very closely similar to the above is figured in black and white by Newman from a specimen in Ingall's collection (Fig. 5, B). [This is apparently the specimen given in *Zoologist*, p. 3304.] Newman, *British Butterflies*, p. 64, fig. A British specimen which nearly approaches this aberration in the absence of the white bars on the costæ and in the absence of the black transverse bar is recorded. In it each of the sub-marginal rows of black spots on the posterior wings is drawn, containing a white spot. In this specimen the brown-red of the type was represented by rose-colour. Newman, *Entomologist*, 1873, p. 345, fig.

Another specimen closely resembling this aberrant form is described from New South Wales. Olliff, A. S., *Proc. Linn. Soc. N.S.W.*, S. 2, III, p. 1250.

Another specimen closely resembling the above was taken at Graham's Town, S. Africa, and is mentioned by Jenner Weir, *Entomologist*, 1889, XXII, p. 73.

Another specimen is figured in which the hind-wings are marked as in the above, but the anterior wings, though strongly resembling this

aberration in the general disposition of the colours, yet differ in details, the chief points of difference being that the white costal bar is only partially obliterated and the white spots on the anal angles of the fore-wings are not developed.

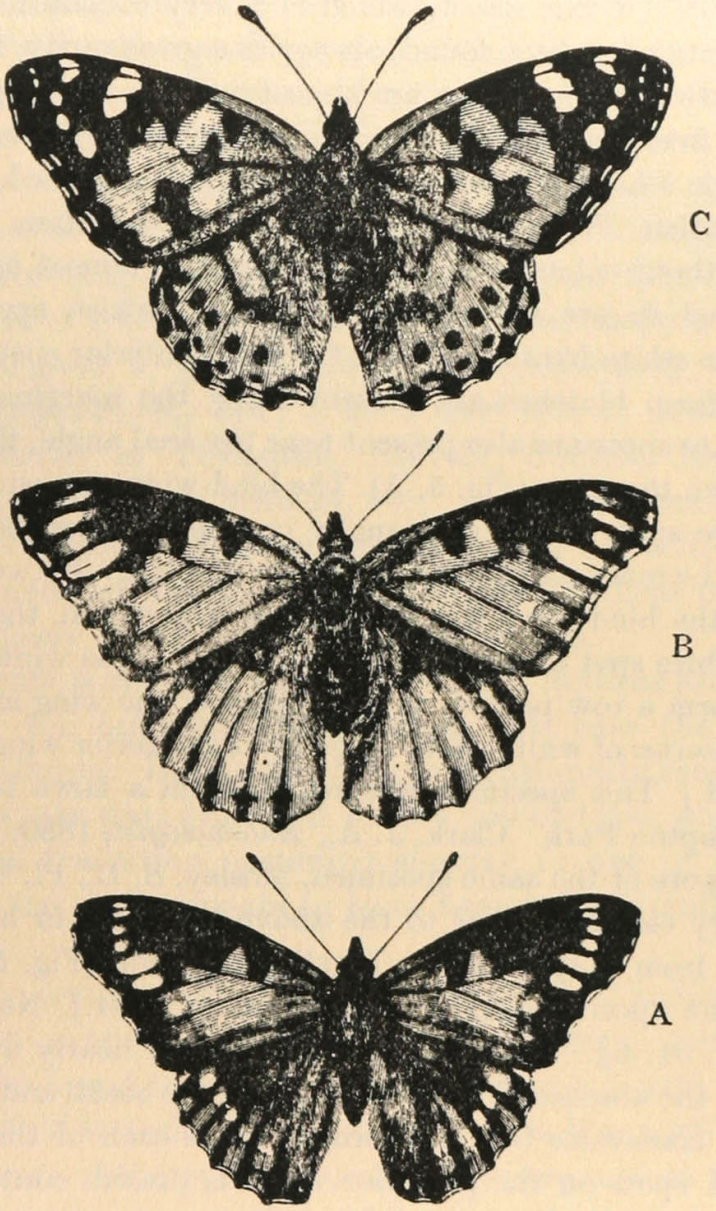


Fig. 5. A. Clark's specimen of *P. cardui*, var. *elymi*, from *Ent.* 1880.
B. Newman's specimen. *Brit. But.* p. 64.
C. *P. cardui*, normal, also from Newman. *Brit. But.* p. 64.

[This specimen was in Kaden's collection and was presumably European.] Herrich-Schäffer, Bd. 1, p. 41, Pl. 35, figs. 157 and 158.

A description is given of an aberrant form taken at King William's Town, S. Africa, which "closely resembled that figured by Herrich-Schäffer." Trimen, R., *South African Butterflies*, 1, p. 201.

A specimen (British) resembling the above, but lacking the white spots on the anal angles of the fore-wings and having the marginal row on the hind-wing light-coloured, but not quite white, is figured by Mosley, Pt. III, Pl. 3, fig. 3.

Two specimens were taken in New Jersey, U.S.A., which are stated to have conformed to this aberration. Strecker, *Cat. N. Amer. Macrolepidop.* p. 137.

Another British specimen generally resembling Herrich-Schäffer's figure is represented by Mosley, Pl. 8, fig. 4.

In all the above specimens the resemblance, as far at least as the upper surface is concerned, is considerable. With the exception of Herrich-Schäffer's example, the undersides are not figured, but from the descriptions it may be gathered that they also resembled each other though probably not so closely as the upper surfaces. The resemblance between the underside of the Australian specimen and that figured by Herrich-Schäffer must have been very close.

"Intermediate between these extreme sports and the normal form are three examples taken at Cape Town in 1866, 1873 and 1874—the first by myself—in which the fore-wing markings are scarcely affected, but the hind-wing spots are minutely ocellate and externally prolonged, so as to be confluent with the succeeding row of lunules." Trimen, *ibid.* pp. 201, 202.

Another aberration, a Belgian specimen, resembles "*Elymi*" in kind but differs from it in degree. In it also the white bars are absent from the costæ, and the brown and black markings of the anterior wings are re-arranged in almost exactly the same manner. The posterior wings are modified to a much less extent and the normal row of black spots between the nervures remains, while only the first and second of the series of white spots is present, the former being very slight. In this individual the markings of the underside also resemble the aberration generally, but it retains the four ocelli of the type. De Donceel, H. Donckier, *Ann. Soc. d'Ent. Belge*, 1878, XXI, p. 10, Pl.

A specimen, also Belgian, is described in which the two anterior wings resemble Herrich-Schäffer's figure in lacking the white bars on the costæ and in the arrangement of the black and ground colour. In neither of them are the white spots of the anal angles (found in the British and Australian specimens) present. The white markings at the apex of the anterior wings differ on the two sides, being in both of them unlike the type and an approach to the aberrations in question, but the degree to which they are developed differs markedly, being greatest on the right side. The *left* posterior wing resembles the aberration in having the six abnormal white spots, but less emphasised than in the figures quoted above; in general colour this wing is darker than the type. The *right* posterior wing, however,

has none of the white spots of the aberration, and differs from the type only in being more suffused with black. To recapitulate, the two anterior and the left posterior wings resemble *generally*, though not entirely, the aberration, while the right posterior wing is nearly normal.

A specimen is described from Ekaterinoslav, S. Russia, which resembles this aberration in wanting the black transverse band and in the disposition of the apical white spots. A trace of the white costal bar remains on the costal border. On the underside of this specimen the ocelli were placed in a pale rose-coloured band. (Name proposed, aberration, *inornata*.) Bramson, K. L., *Ann. Soc. Ent. France*, S. 6, VI, 1886, p. 284.

Besides the rare aberration "var. *Elymi*," there is a variety sometimes found in Europe, which in Australia is so constant and definite that it has been regarded as a species. The following may be quoted respecting its occurrence in Australia, where it is common:

"There is in abundance about Melbourne and in many other parts of Australia a *Cynthia* with the general appearance and habit of *C. cardui*, so closely represented that every entomologist I know refers it to that species. The Australian species differs from the European one constantly, however, in having the centres of the three lower round spots on the posterior wings bright blue, and having two other blue spots on the posterior angles of the same wings, the corresponding parts of the European form being black." For this form the name *C. kershawi* is proposed. M'Coy, F., *Ann. and Mag. of Nat. Hist.* Ser. 4, I, 1868, p. 76. See also Olliff, A. S., *Proc. Linn. Soc. N.S.W.* Ser. 2, III, p. 1251. The notices of its occurrence in Europe are as follows. In 1884 Mr Jenner Weir exhibited a specimen of *P. cardui*, taken in the New Forest. Three of the five black spots in the disk of the upper side of the hind-wings had blue pupils; he pointed out that the specimen thus approached the Australian form, *P. kershawi*. *Proc. Ent. Soc.* 1884, p. xxvii.

Olliff, *loc. cit.*, states that he has taken a specimen having these blue markings at Katwijk, in Holland.

In the case given, the evidence certainly suggests that these various forms of aberration are grouped round a normal form of aberration, just as the individuals of the type are grouped round its normal.

One example of a similar discontinuity in a melanic Variation may profitably be given. I have taken this opportunity of referring to such a case, as the general evidence of melanic Variations goes on the whole to show that they are not commonly discontinuous, and further

evidence on this point would be most valuable. To appreciate the evidence Butler's coloured plate should be referred to.

Terias. A well-marked group of butterflies of this genus allied to *T. hecabe* is found in Japan. It contains forms of great diversity in amount of black border which occurs on the outer margins of the fore- and hind-wings. The remainder of the wings is lemon-yellow. The black border may be confined to the tip of the fore-wings, or may there occupy a considerable area and be extended along the whole outer margin of both wings. The form with the least black is called *T. mandarina*, that with the most is called *T. mariesii*, and the intermediate form is called *T. anemone*. Upwards of 150 specimens, all from Nikko, were examined; these ranged between the two extremes, and were found to form a continuous series. Butler states that "the absence of six of them, referable only to two gradations, would at once leave the three species as sharply defined as any in the genus."

[In the case of these butterflies there are thus three groups of varieties, two extreme groups and one mean group; intermediates between these are comparatively rare. Butler suggests that these intermediate forms should be regarded as hybrids, even in the absence of experimental evidence. This view is of course dependent on the truth of the belief that such a discontinuous occurrence of variations is anomalous.]

Twenty specimens of the species *T. betheseba* and thirty-nine of *T. jaegeri* (both of Japan) were also examined. The former presented no variations whatever, and the latter only vary in the yellower or redder tint on the under surface of the secondaries. Butler, A. G., *Trans. Ent. Soc.* 1880, p. 197, Pl. VI.

Compare the following:

Terias constantia. Twenty-five pupæ, all found together on the same twigs at Teapa, Tabasco, Mexico, by Mr H. H. Smith. The butterflies from these are in Messrs Godman and Salvin's collection, who kindly allowed me to examine them. The amount of black border on both wings varies much, nearly though not quite so much as in the cases figured by Butler. In the lightest the apex of the fore-wing alone is black, and there is no black on the hind-wing in 9 specimens; of the remaining 16 some have a well-defined black border to the hind-wing, while in the rest (about 6) this border is slight. This case is a particularly interesting one, as the specimens were associated and presumably belonged to one brood.

For another beautiful case of discontinuous Variation in pattern I am indebted to Dr D. Sharp. The Cambridge University Museum lately received a series of 38 specimens of *Kallima inachys*, the well-

known butterfly whose folded wings resemble a dead leaf with its mid-rib and veinings. The underside of this butterfly is sometimes marked with large blotches and flecks of irregular shape, which, as has often been noted, resemble the patches of discoloration caused by fungi in decaying leaves. Dr Sharp pointed out to me that the specimens examined fell naturally into four groups according to the coloration of the underside. In the first group the field is nearly plain, though the tint varies in individuals. The "mid-rib" is strongly marked in this and all the groups, but the "veinings" are absent or very slightly marked in the first group: 18 specimens. In the second group the ground is almost plain, but it bears numerous strongly marked black-speckled spots, of forms which though irregular in outline are closely alike, and occupy the same positions in all the six specimens, being scarcely if at all represented in any of the others. In the third group the dark bars representing "veins" are strong, but the field is nearly uniform: 10 specimens. In the fourth group, of four specimens, the ground-colour is darkened in such a way as to leave large and definite blotches of light colour in particular places. Of these specimens three have the veinings very strongly marked, while the fourth is without them.

Into these four groups the specimens could be unhesitatingly separated, though in each group many individual differences occurred. No marked Variation in the upper-sides was to be seen. These specimens were all from the Khasia hills, Assam, but there was of course no evidence that all were flying together.

One of the most interesting examples of discontinuous Variation in colour-patterns is the case of ocellar markings or eye-spots. Upon this subject nothing need here be said as the evidence will be given in detail in the course of this volume (see Chap. XIII).

SECTION X

Discontinuity in Substantive Variation.—Miscellaneous Examples

Of the discontinuous occurrence of Substantive Variation, the manifestations are many and diverse. We have seen that in such features as size, colour, and colour-patterns, Variations may be discontinuous, and a form may thus result, differing markedly from the type which begot it. Variation in the proportions or the constitution of essential parts may no less suddenly occur. The range of

these phenomena is a large one, but for the purposes of this Introduction a few examples must suffice in general illustration of their scope.

A discontinuous Variation which is familiar to all is that of "reversed" varieties, especially of molluscs and flat-fishes. Such varieties are formed as optical images of the body of the type. In both of the groups named, some species are normally right-handed, others being normally left-handed, while as individual Variations reversed examples are found. In molluscs this is not peculiar to Gasteropods with spiral shells, but may occur also both in Limacidæ (slugs)[1] and in Lamellibranchs[2]. Such Variation is commonly discontinuous, and the two conditions are alternative. The fact that the reversed condition may become a character of an established race is familiar in the case of *Fusus antiquus*. This shell is found in abundance as a fossil of the Norwich Crag, such specimens being normally left-handed, though the same species at the present day is a right-handed one. Of the left-handed form a colony was discovered by MacAndrew on the rocks in Vigo Bay[3]. It was there associated with certain other shells proper to the Norwich Crag. This discovery seemed to Edward Forbes to be so remarkable that he looked on it as corroborative evidence of a special connection between the fauna of Vigo Bay and the Crag fossils[3]. Jeffreys had the same variety from Sicily[4].

That they may the better serve to bring out the significance of Discontinuity in Variation to the general theory of Descent, it may be well to choose some examples with reference to characters which when seen in domestic animals are looked on as especially the result of Selection.

In exoskeletal structures several of this kind are known. From time to time there have been records of captures of the "hairy variety" of the moorhen (*Gallinula chloropus*), in which the feathers were destitute of barbules and consequently had a hairy texture, greatly changing the general appearance of the bird.

Of the "hairy" variety twelve specimens were recorded, five from Norfolk, and the rest from Cambridgeshire, Hampshire, Sussex (2), Suffolk, Nottinghamshire and Athlone in Ireland. The tips of the barbs

[1] For example, a sinistral *Arion*, Baudon, *Jour. de Conch.* XXXII, 1884, p. 320, and many others.

[2] Sinistral *Tellina*, Fischer, P., *Jour. de Conch.* XXVIII, 1880, p. 234. The same is recorded in several other genera.

[3] Seven specimens, *Ann. N.H.* 1849, p. 507.

[4] *Brit. Conch.* I, p. 326.

and shafts of the feathers have been broken off and the barbules are entirely wanting, giving a hairy appearance. This appearance was found in the whole of the plumage. Owing to the absence of barbules, the general coloration is tawny. A few feathers of this kind have been found in hawks and gulls, and in the case of a *Parra* (a bird which bears considerable resemblance to a moorhen), lent to Mr Gurney by Prof. Newton, a great portion of the body feathers were in this condition. The feathers of the *Apteryx* and Cassowary are also partially destitute of barbules. Mr Gurney was informed of a single case of a grey Brahma hen which showed the same peculiarity which appears otherwise to be without parallel. The case of the silky fowl is similar in the absence of most of the barbules, but in it the point of the shaft is produced to a delicate point, and the barbs are fine and sometimes bifid or trifid at the apex. From J. H. Gurney, *Trans. Norwich Nat. Soc.* III, p. 581, Pl. [Bibliography given.] [If another "hairy" moorhen is found, note of the colour of the skin and bones should be made, for, as is well known, in the silky fowl they are purplish blue.]

The following may be compared: "Cochins are now and then met with in which the webs of the feathers having no adhesion, the whole plumage assumes a silky or flossy character like that of the silky fowl. It usually occurs quite accidentally, and in every case we have met with, the variety has been buff. By careful breeding the character can be transmitted, but we have only known *one* case in which there had been this hereditary character, the others having been of accidental occurrence. Such birds are sometimes called 'emu' fowls." Lewis Wright, *Illust. Book of Poultry*, 1886, p. 230.

Of many domestic animals, for example, the goat, cat and rabbit, varieties with long, silky hair are familiar under the name of "Angoras." Very similar breeds of guinea-pigs are kept, to which the name "Peruvian" is given. In this connection the capture of a mouse (*Mus musculus*) with long, black, silk-like hair is interesting[1], as showing that such a total Variation may occur as a definite phenomenon without Selection.

As to the partial nakedness of the skin of many animals (Man, etc.), several suggestions have been made. It has been variously supposed that the covering of hair has been gradually lost by Man, in correlation with the use of clothes; with the heat of the sun; for ornamental purposes under sexual selection[2]; or perhaps as a protection from

[1] Cocks, W. P., *Trans. Cornwall Polytech. Soc.* 1852. Like other animals, mice have of course often been found black. For instance, a number of black mice were found in Hampstead-down Wood. Hewett, W., *Zool. Journ.* IV, p. 384.

[2] C. Darwin, *Descent of Man*, I, p. 142.

parasites[1]. Various suggestions have also been made to explain the persistence of hair at the junction of the limbs and on the head and face. To a consideration of the origin of nakedness, the evidence of Variation in some measure contributes, and though the bearing is not very direct, it may illustrate the futility of inquiries of this kind made without regard to the facts of Variation.

Mouse (*Mus musculus*): male and pregnant female found in a straw-rick at Taplow; both were entirely naked, being without hairs at all, excepting only a few dark-coloured whiskers. The skin was thrown up into numerous prominent folds, transversely traversing the body in an undulating manner. This condition of the skin obtained for them the name of "rhinoceros mice." The ears were dark or blackish, the tail ash-coloured, and the eyes black, indicating that they were not albinos. The exfoliations from the skin were examined microscopically but no trace of hair-follicles was found nor any suggestion of disease. The animals were active and healthy.

The young ones, when born, were similar to the parents. The teeth were normal.

In the Museum of the College of Surgeons is a precisely similar specimen which was found in a house in London. Gaskoin, *Proc. Zool. Soc.* 1856, p. 38, Pl.

Three specimens of the common mouse (*Mus musculus*) were caught in the town of Elgin. The whole bodies of these three creatures "were completely naked—as destitute of hair and as fair and smooth as a child's cheek. There was nothing peculiar about the snout, whiskers, ears, lower half of the legs and tail, all of which had hair of the usual length and colour. They had eyes as bright and dark as in the common variety....At least two others were killed in the same house where these were found." Gordon, G., *Zoologist*, 1850, VIII, p. 2763.

Shrew. (*Sorex* sp.) "whole of upper surface of head and body destitute of hair, and skin corrugated like that of naked mice figured in *P.Z.S.* 1856"; sent to Brit. Mus. by Mr P. Garner. Gray, J. E., *Ann. and Mag. of N.H.* 1869, S. 4, IV, p. 360.

In connection with these cases, the following fact is interesting:

Heterocephalus is a genus of burrowing rodent from S. Africa. It contains two species, of which one is about the size of a mouse and the other is rather larger. They are characterised by possessing an apparently hairless skin which is on the head and body of a wrinkled and warty nature. On closer inspection the skin is seen to be furnished with fine scattered hairs,

[1] Belt, *Naturalist in Nicaragua*; see also Hudson, *Naturalist in La Plata*, 1892.

but there is no general appearance of a hairy covering. There is no external ear in these animals. Oldfield Thomas, *P.Z.S.* 1885, p. 845, Pl. LIV.

Naked horses have often been exhibited. Such a horse caught in a semi-feral herd in Queensland was described by Tegetmeier, *Field*, XLVIII, 1876, p. 281. The skin was black and like india-rubber. Careful examination showed no trace of hair, or any opening of a hair-follicle. In Turkestan, in the year 1886, I heard of one thus travelling, but failed to see it. "Hairless" dogs in S. America remain distinct (Belt, *l.c.*).

Of discontinuous Substantive Variation in bodily proportions a single example must suffice. Among domestic animals of many kinds, races are known in which the bones of the face do not grow to their full size, while the bones of the jaw are, or may be, of normal proportions. Familiar examples of this are the bull-dog, the pug, the Japanese pug, the Niata cattle of La Plata[1], some short-faced breeds of pigs, and others. In the case of these domestic animals the part which Selection has taken in their production is unknown, and the magnitude of the original Variations cannot be ascertained. It is nevertheless of interest to notice that parallel Variations have occurred in distinct forms, and I think that this is to some extent evidence that the Variations were from the first definite and striking. As regards the dogs even, there is a presumption that the short face of at least the Japanese pug arose independently from that of the common, or Dutch pug (as it used to be called), but as to this the evidence is insufficient. Among the dogs' skulls found in ancient Inca interments, a skull was found having the form of the bull-dog. Nehring, *Kosmos*, 1884, XV. As these remains belong to a period before the European invasion, it is most probable that this bull-dog breed arose independently of ours.

Apart, however, from domestic animals there is evidence as to the origin of short-faced breeds. This evidence, which is not so well-known as it deserves to be, is provided by the occurrence of a similar Variation in fishes. Darwin in speaking of the evidence as to Niata cattle makes allusion to the case of fishes in a note[2], quoting Wyman as to the cod, which occurs in a form known to fishermen as the "bull-dog" cod. The interest of this observation is increased by the fact that it does not stand alone, but similar Variations have been seen in the carp, chub, minnow, pike, mullet, salmon and trout. In

[1] C. Darwin, *Animals and Plants under Domestication*, 2nd ed. I, p. 92.

[2] *Ibid.* p. 93, *note*.

the last-named there is even evidence of the establishment of a local race having this singular character.

Carp (*Cyprinus carpio*). "Bull-dog"-headed carp have often been described. The face ends more or less abruptly in front of the eyes, while the lower jaw has almost its normal length. The front part of the head is bulging and prominent, giving the fish an appearance which several authors compare to that of a monumental dolphin. A good figure of such a specimen is given by G. St Hilaire, *Hist. des Anom.* ed. 1837, I, p. 96, where a full account of the older literature of the subject may be found. Inasmuch as carp are largely bred in ponds on the Continent, there is in this case some suggestion that unnatural conditions may be concerned, but this suggestion does not apply to other cases of the same Variation. Otto, *Lehrb. path. Anat.* I § 129, states that in the ponds of Silesia such fish are not rare. See also Voigt, *Mag. f. d. Naturk.* III, p. 515.

Cyprinus hungaricus: specimen from the Danube similarly formed. The forehead was protuberant and bulged in front of the eyes so that its anterior border was almost vertical. The attachments of the mandible are carried forward in such a manner that the mandible itself was directed upwards almost at right angles to the body. [Good figure.] Steindachner, *Verh. zool.-bot. Ges. Wien*, 1863, XIII, p. 485, Pl.

[Several other types of Variation in the heads of Cyprinoids occur, but cannot be described here.]

Chub (*Leuciscus dobula* = *cephalus*): specimen having anterior part of head rounded "like a monumental dolphin." The body was normal, measuring 33 cm. in length. Landois, *Zool. Garten*, 1883, XXIV, p. 298.

Minnow (*Phoxinus lævis*) specimen having a snout like a pug ("*museau du mopse*") [no description]. Lunel, *Poiss. du lac Léman*, p. 96.

Mullet (*Mugil capito*): specimen having both jaws directed upwards, and the upper and anterior parts of the skull greatly elevated and protuberant: the appearance of the head was like that of a pug dog. Full measurements given. Canestrini, R., *Atti della soc. Ven.—Trent. di sci. nat. in Padova*, 1884, IX, p. 117 [Bibliography given].

Pike (*Esox lucius*) described as like a pug, *ibid.* p. 124; see also Vrolik's *Atlas*, 1849, *Tab.* LXI, fig. 6.

Salmon (*Salmo salar*): specimen having front part of face little developed, the supra-maxillaries being asymmetrical. Lower jaw projects far in front of upper jaw. Animal of fair size, and not meagre. Van Lidth de Jeude, *Notes from Leyden Mus.* VII, p. 259, Pl. [Curious malformation of *S. trutta ibid.*], see also *Jahrb. Ver. vaterl. Nat. Württ.* XLII, p. 345.

Trout (*S. fario*): several specimens having bull-dog heads were taken in Lochdow, near Pitmain, Inverness-shire. Heads short and round; upper

jaw truncated like a bull-dog. This variety does not occur in neighbouring lochs. None weighed more than ½ lb. Yarrell, *Brit. Fishes*, I, p. 286, figure given.

Another specimen (Fig. 6), agreeing closely with Yarrell's figure, was taken in a lake at an altitude of 6000 ft. in the valley of Sept-Laux (Isère). Saving the head it was in all respects normal. This specimen is described and figured by Carlet, M. G., *Journ. de l'Anat. et Phys.* 1879, XV, p. 154. [It is declared that the fishermen who took it, having previously met with similar specimens, supposed that they had found a new species, but it is not expressly stated that these other specimens were from the same locality.]

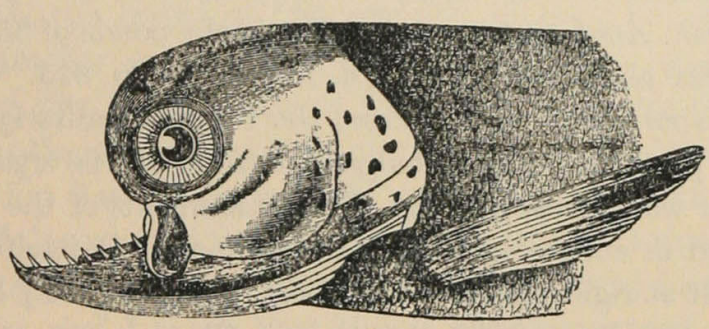


Fig. 6. Bull-dog-headed trout, after Carlet.

Before ending this preliminary glance at Discontinuity in Substantive Variation, allusion must be made to a case which is at once more famous and more instructive than any other. I refer to the celebrated phenomenon of the production of nectarines by peaches, or conversely. Upon the subject of almond, peach and nectarine, Darwin produced a body of facts which, whether as an example of a method or for the value of the facts themselves, form perhaps the most perfect and the most striking of all that he gave.

The evidence which is there collected is known to all, and though similar observations have been made since by many, there is I believe nothing of importance to add to Darwin's statement. The bearing of these phenomena on the nature of Discontinuity in Variation is so close that Darwin's summary may with profit be given at length.

"To sum up the foregoing facts; we have excellent evidence of peach-stones producing nectarine-trees, and of nectarine-stones producing peach-trees—of the same tree bearing peaches and nectarines —of peach-trees suddenly producing by bud-variation nectarines (such nectarines reproducing nectarines by seed), as well as fruit in part nectarine and in part peach,—and, lastly, of one nec-

tarine tree first bearing half-and-half-fruit and subsequently true peaches[1]." After disposing of alternative hypotheses he concludes that "we may confidently accept the common view that the nectarine is a variety of the peach, which may be produced either by bud-variation or from seed."

In this case the evidence is complete. The Variation from peach to nectarine or from nectarine to peach may be *total*. If less than total, the fruit may be divided into either halves or quarters[2], so that for each segment the Variation is total still. Of intermediate forms other than these divided ones, we have in this case no evidence: it is therefore a fair presumption that they are either rare or non-existent; and that the peach-state and the nectarine-state are thus positions of "Organic Stability," between which the intermediate states, if they are chemical and physical possibilities, are positions of instability.

These examples of Discontinuity in Substantive Variation must suffice to illustrate the nature of the phenomena. It will be seen that the matters touched on cover a wide range, and the evidence relating to them must be considered separately and at length. Such a consideration I hope in a future volume to attempt.

SECTION XI

Discontinuity in Meristic Variation: Examples

Inasmuch as the facts of Meristic Variation form the substance of this volume, it is unnecessary in this place to do more than refer to the manner in which they exhibit the phenomenon of Discontinuity. One or two instances must suffice to give some suggestion of this subject, detailed consideration being reserved.

Parts repeated meristically form commonly a series which is either radial or linear, or disposed in some other figure derived from or compounded of these. For the purpose of this preliminary treatment an instance of Discontinuous Variation in each of these classes may be taken.

[1] *Animals and Plants under Domestication*, ed. 2, I, p. 362.

[2] *Ibid.* p. 362, quoting from *Loudon's Gard. Mag.* 1828, p. 53. The case of a Royal George peach which produced a fruit, "three parts of it being peach and one part nectarine, quite distinct in appearance as well as in flavour." The lines of division were longitudinal.

1. *Radial Series*

Variations in the number of petals of actinomorphic flowers exhibit the Discontinuity of Meristic Variation in perhaps its simplest form.

Phenomena of precisely similar nature will hereafter be described in animals, but such Variations in flowers are so common and so accessible that reference to them may with profit be made. In Fig. 7 such an example is shown.

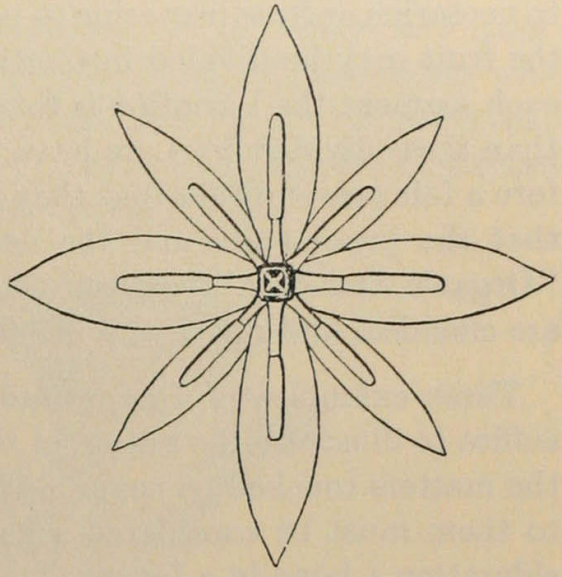


Fig. 7. Diagram of the flower of a tulip having all the parts in -4.

It represents a tulip having the parts of the flower formed in multiples of four, instead of in multiples of three as normally. Variation of this kind may be seen in any field or hedgerow[1].

Meristic Variation is here presented in its greatest simplicity. Such a case may well serve to illustrate some of the phenomena of Discontinuity.

A form with four segments occurs as the offspring of a form with three segments. Such a Variation, then, is discontinuous because a new character, that of division into four, has appeared in the offspring though it was not present in the parent. This new character is a definite one, not less definite than that of division into three. It has come into the strain at one step of Descent. Instances in which there is actual evidence of such descent are rare, but there can be no question that these changes do commonly occur in a single generation, and, indeed, in many plants, as for example *Lysimachia* (especially *L. nemorum*), flowers having all the parts in -4 or in -6 may be frequently seen on plants which bear likewise normal flowers with the parts in -5.

Now such a Variation as this of the tulip illustrates a phenomenon which in the Study of Variation will often be met.

We have said that the Variation is discontinuous, meaning thereby

[1] For full literature and lists of cases see especially Masters, *Vegetable Teratology*, s.v. *Polyphylly*. It is perhaps unnecessary to refer to the fact that the numerical changes here spoken of are quite distinct from those which result from an assumption by the members of one series or whorl of the form and characters proper to other whorls.

that the change is a large and decided one, but it is more than this; it is not only large, it is *complete*.

The resulting form possesses the character of division into four no less completely and perfectly than its parent possessed the character of division into three. The change from three to four is thus perfected: from the form with perfect division into three is sprung a form with perfect division into four. This is a case of a *total* or *perfect* Variation.

This conception of the totality or perfection of Variation is one which in the course of the study will assume great importance, and it may be best considered in the simple case of numerical and Meristic Variation before approaching the more complex question of the nature of totality or perfection in Substantive Variation.

The fact that a Variation is perfect at once leads to the question as to what it might be if imperfect. Between the form in -3 and the form in -4 are intermediates possible? and if possible, do they exist? Now by choosing suitable species of regular flowers, individual flowers may no doubt be found in which there are three large segments and one small one; or two normal segments and a third divided into two, making four in all. Such flowers are firstly rare, while cases of perfect transformation are common. But besides their rarity there is, further, a grave doubt whether they are in any true sense *intermediate* between the perfect form in -3 and the perfect form in -4. After this again it must be asked whether or no they do as a matter of fact occur as intercalated steps in the descent of the form in -4 from the form in -3? To the last question a general negative may at once be given; for though there is abundant evidence that Meristic Variations of many kinds and in several degrees of completeness may be seen in the offspring of the same parent, yet any one member of such a family group may show a particular Variation in its perfection, and the occurrence of any intermediate in the line of Descent is by no means necessary for the production of the perfect Variation.

To answer the former question, whether or no forms imperfectly divided into four parts are in reality intermediate between those in -3 and those in -4, a knowledge of the mechanics of the process of Division is required. Such knowledge is as yet entirely wanting, and discussion of this matter must therefore be premature. With much hesitation I have decided to make certain reflections on the subject, which will be found in an Appendix to this work. These may perhaps have a value as suggestions to others, though from their theoretical nature they can find no place here.

There is however another class of cases which are intermediate in a different way. In the tulip described above the quality of division into 4 was present in all the floral organs. This is not always the case, for a Meristic Variation may be present in one series of organs, though it is absent in some or all of the others, and this is a phenomenon frequently recurring. Nevertheless, though only partially distributed, a Variation may still be displayed in its totality in the parts wherein it is present. The parts of a single whorl, the calyx for example, may undergo a complete Variation, while the corolla and other parts are unchanged. In the same way single members of a radial series, as a petal for example, may undergo a complete Variation while the other members of the series are unchanged. The same will be shown hereafter to be true of animals also.

For instance, the normal number of the parts in the disc of *Aurelia* is four, but the whole body may be divided into six or some other number of parts. Examples are also found in which the parts of one-half or of one quadrant are arranged in the new number, while the remainder is normal; and, as in flowers, this new number may prevail in some or in all of those systems of organs which are disposed around the common centre.

2. *Linear Series*

Before speaking further of the totality or perfection of Variation it will be well to give an illustration of Discontinuous Meristic Variation as it occurs in the case of a linear series of parts. As such an illustration the case of the Variation in the number of joints in the tarsus of the cockroach (*Blatta*) may be taken. This Variation has been the subject of very full investigation by Mr H. H. Brindley. The tarsus of the cockroach is normally divided into five joints, but in about 25 per cent. of *B. americana* (and in a smaller proportion of several other species) the tarsus of one or more legs is divided into only four joints, though the total length may be the same as that of the corresponding leg of the other side, Fig. 8. Between the five-jointed form of tarsus and the four-jointed form no single case in any way intermediate was seen. The whole evidence will be given in full in the proper place and raises many questions of great interest; but that which is important to our present consideration is the fact that the Variation is here undoubtedly discontinuous, arising suddenly as a total or perfect Variation, from the five-jointed form to the four-jointed. Here the Variation, though total as regards the limb in which

it is present, is not total as regards all the legs taken together. For commonly only a single leg had a four-jointed tarsus, and only one specimen was met with in which all six legs thus varied, and one specimen only showed the Variation in five legs.

In speaking of such a Variation as a *perfect* Variation several things are meant.

First, it is meant that the tarsus of the new pattern is as distinctly divided into four joints as the normal is into five. In addition to this the statement that the varying limb is perfect conveys a number of ideas that cannot be readily formulated; for example, that the joints are to all appearances properly proportioned and serviceable, showing no sign of unfitness: they have in fact much the same appearance as

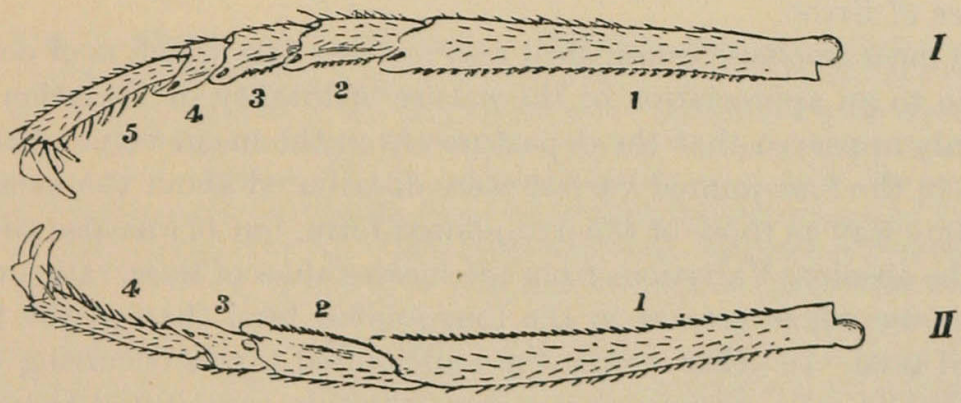


Fig. 8. Tarsi of the third pair of legs in a specimen of *Blatta americana*. I. the left tarsus, having the normal, or 5-jointed form; II. the right tarsus, having the 4-jointed form.

they have in those of the Orthoptera in which the tarsus is normally four-jointed. But besides these attributes, which though useful enough for ordinary description are still in their nature formless and of no precise application, there is another which in the case of these varying legs we are entitled to make. We have said that these four-jointed tarsi are to all appearance normal, save for the number of the joints. Now the measurements which, at my suggestion, Mr Brindley has been kind enough to make, entitle us to go beyond this, and to assert that the four-jointed tarsus has another character by reason of which it is actually in a sense a "normal" form. A brief consideration of this will clearly illustrate the meaning of the term "perfection" applied to Variation.

We saw above that in a monomorphic form, the frequency with which, in respect of any given character, it departs from its mean condition follows a curve of Frequency of Error. This is, indeed, what is meant by the statement that the mean condition is a normal.

Taking the five-jointed tarsus, measurements showed that the ratio of the length of any given joint to the length of the whole tarsus varied in this way about a mean value. Measurement of the joints of the four-jointed form showed that the ratios which they bear to the total length of their respective tarsi vary in a similar way about their mean values, and that there is thus a "normal" four-jointed condition just as there is a "normal" five-jointed condition. In the same way, then, that the ratio of the length of each of the five joints to that of the whole tarsus is not always identical but exhibits small Variations, so the ratios of the several joints of the four-jointed tarsus to the length of the whole tarsus also vary, but in each case the ratio has a mean value which is approached with a frequency conforming to a curve of Error.

The measurements established also another fact which is of consequence to an appreciation of the nature of totality in Variation. It not only appeared that the departures from the mean value of these ratios in the four-jointed variety were distributed about the mean in the same way as those of the five-jointed form, but it was also shown that the absolute Variations from the mean values of these ratios were not on the whole greater in the four-jointed tarsi than in the five-jointed tarsi. In other words, the four-jointed tarsus occurring thus sporadically, as a variety, is not less definitely constituted than the five-jointed type, and the proportions of its several joints are not less constant. It is scarcely necessary to point out that these facts give no support to the view that the exactness or perfection with which the proportions of the normal form are approached is a consequence of Selection. It appears rather that there are two possible conditions, the one with five joints and the other with four, either being a position of Organic Stability. Into either of these the tarsus may fall; and though it is still conceivable that the final choice between these two may have been made by Selection, yet it cannot be supposed that the accuracy and completeness with which either condition is assumed is the work of Selection, for the "sport" is as definite as the normal.

This interesting case of Meristic Variation in the tarsus of the cockroach illustrates in a striking way the principle which is perhaps the chief of those to which the Study of Variation at the outset introduces us. We are presented with the phenomenon of an organ existing in two very different states, between which no intermediate has been seen. Each of these states is definite and in a sense perfect and complete; for the oscillations of the four-jointed form around its mean

condition are not more erratic than those of the normal form. Now when it is remembered that just such a four-jointed condition of the tarsus is known as a normal character of many insects and especially of some Orthoptera, it is, I think, difficult to avoid the conclusion that if the four-jointed groups are descended from the five-jointed, the Variation by which this condition arose in them was of the same nature as that seen as an individual Variation in *Blatta*; that as the modern phenomenon of the individual Variation which we see, so that past phenomenon of the birth of a four-jointed race, was definite and complete, and that the change whose history is gone, like the change to be seen to-day, was no gradual process, but a Discontinuous and total Variation[1].

[1] Since this Section was written it has seemed possible that the account given above may be found to need an important modification. It is well known that *Blatta*, in common with many other Orthoptera, has the power of reproducing the antennæ and legs after amputation or injury, and we have made some observations showing that the tarsi of these regenerated legs sometimes, if not always, contain *four* joints. The question therefore arises whether the four-jointed tarsus is a truly congenital Variation, and not rather a Variation introduced in the process of regeneration, somewhat after the manner of a bud-variation. To determine this point a considerable number of immature specimens were examined, and it was found that the percentage of individuals with four-jointed tarsi is considerably less in the young than in the adult. These facts lend support to the view that the four-jointed condition is not congenital. A quantity of individuals were also hatched from the egg-cocoons, and among them there has thus far been found no case of four-jointed tarsus. On the other hand the total number thus hatched is not yet sufficient to create any strong probability that none are ever hatched in the four-jointed state. We have also seen the four-jointed tarsus in three very young individuals, which, to judge from their total length, must have been newly hatched. The statistics show besides that the abnormality is distinctly commoner in females than in males, and that it is commoner in the legs of the second pair than in the first, and much more common in the third pair of legs than in the second. These facts somewhat favour the view that the Variation may be congenital. It seems also exceedingly improbable that in the specimen with all the tarsi four-jointed, the six legs could each have been lost and renewed. There seems on the whole to be a presumption that the Variation may at least sometimes be congenital. Supposing however that this shall be found hereafter not to be the case, I do not think that the deductions drawn from the facts will be less valid. The conclusions as to the definiteness of the two types, and the relationships of the several parts of each to the several parts of the other, would still hold good. There are besides in other forms instances of similar numerical Variation, as for example, in the number of joints in the antennæ of Prionidæ, where the hypothesis of change on renewal is impossible, from which a similar argument might be drawn; but on the whole I have preferred to leave the account as it stands, taking the case of *Blatta* as an example, because it is easily accessible and because, from the fewness of the joints concerned, the issues are singularly clear.

SECTION XII

Parallel between Discontinuity of Sex and Discontinuity in Variation

The application of the term Discontinuity to Variation must not be misunderstood. It is not intended to affirm that in discontinuous Variation there can be between the variety and the type no intermediate form, or that none has been known to occur, and it is not even necessary for the establishment of Discontinuity that the intermediate forms should be rare relatively to the perfect form of the variety, though in cases of discontinuous Variation this is generally the case; but it is rather meant that the perfect form of the variety *may* appear at one integral step in Descent, either without the occurrence of intermediate gradations, or at least without the intercalation of such graduated forms in the pedigree.

In the case of the tarsus of *Blatta* we have seen an example of a total and complete Variation affecting single members of a series of repeated parts, not collectively, but one or more at a time[1]. Such an instance of a Meristic Variation occurring in a state which is total as regards members of a series but not total as regards the whole series finds many parallels among Substantive Variations, as, for example, that of the crab (*Cancer pagurus*) bearing the right third maxillipede fashioned as a chela, while the left third maxillipede was normal. Variations of this nature in plants are of course well known to all.

At a previous place (Section VII) allusion was made to the familiar but very curious analogy between members of a series of Meristic parts and separate organisms. The facts of Variation bring out this analogy in many singular ways, and in speaking of the totality of Variation it is necessary to bear these facts in mind. Not only are there abundant instances of independent division or multiplication of single members of Meristic series, but, as has been said, single members of such series may thus independently and singly undergo qualitative or Substantive Variation, being treated in the physical system of the body as though they were separate units. In Variation, therefore, though it will be found that members of Meristic series *may* vary simultaneously and collectively—and this is one of the most important generalisations which result from the Study of Variation—yet it is also true that in Variation single members of such series *may* vary

[1] See Note at the end of Section XI.

independently and behave as though they possessed an "individuality" of their own. If ever it shall be possible to form a conception of the physical processes at work in the division and reproduction of organisms, account must be taken of both of these phenomena.

I know no way in which the nature of Discontinuity in Variation and the position of intermediate forms may be so well illustrated as by the closely parallel phenomenon of Sex. In the case of Sex in the higher animals we are familiar with the existence of a race whose members are at least dimorphic, being formed either upon one plan or upon the other, the two plans being in ordinary experience alternative and mutually exclusive. Between these two types, male and female, there are nevertheless found intermediate forms, "hermaphrodites," occurring in the higher animals, at least, as great rarities. Now though these intermediate forms perhaps exist in gradations sufficiently fine to supply all the steps between male and female, it cannot be supposed that the one sex has been derived from the other, and still less that the various stages of hermaphroditism have been passed through in such descent. Besides this, even though there is an accurate correspondence or homology between the several organs which are modified upon the one plan in the male and upon another in the female, and though this homology is such as to suggest, were we comparing two species, that the one had been formed from the other, part by part, yet by the nature of the case such a view is here inadmissible: for firstly it is impossible to suppose that either sex has at any time had the organs of the other in their completeness, and secondly it is clear that any hypothetical common form, by modification of which both may have arisen, must have been indefinitely remote and could certainly not have possessed secondary sexual organs bearing any resemblance to those now seen in the higher forms. All this has often been put, but the application of it to Variation is of considerable value. For in the case of Sex there is an instance of the existence of two normals and of many forms intermediate between them, occurring in a way which precludes the supposition that the intermediates represent stages that have ever occurred in the history of the two forms.

In yet another way Sex supplies a parallel to Variation. As we know, the sexes are discontinuous and occur commonly in their total or perfect forms. Now just as members of a Meristic series may present total Variations independently of each other, so may single members of such a series present opposite secondary sexual characters,

which may nevertheless be in each case complete. The best known instance of this is that of gynandromorphic insects, in which the characters of the whole or part of one side of the body, wings and antennæ, are male, while those of the other side are female. Remarkable instances of a similar phenomenon have been recorded among bees and will be described later. As is well known, the organs and especially the legs of the sexless females or workers are formed differently from those of the drones, but there are cases of individuals having some of the parts and appendages formed on the one plan and some on the other. Thus in these individuals, which are in a sense intermediate between workers and drones, the characters of the two sexes may still be not completely blended, the male type prevailing in some parts, and the female in others. In the Discontinuity of Substantive Variation will be found examples of imperfect blending of variety and type closely comparable with this case of the imperfect blending of Sex.

SECTION XIII

Suggestions as to the Nature of Discontinuity in Variation

The observations at the end of Section XI regarding the Discontinuity of Meristic Variation lead naturally to certain reflections as to the nature of Discontinuous Variation in general. In the case of the cockroach tarsus, there given, it appeared that just as the structure of the typical form varies about its mean condition, so the structure of the variety varies about another mean condition. This fact, which in the given instance of Meristic Variation is so clear, at once suggests an inquiry whether this is not the usual course of Discontinuous Variation, and, indeed, whether Discontinuity in Variation does not mean just this, that in varying the organism passes from a form which is the normal for the type to another form which is a normal for the variety. Such transitions plainly occur in many cases of Meristic Variation, and in a considerable number of Substantive Variations there will be found to be indications that the phenomenon is similar. It is true that at the present stage of the inquiry the evidence has the value rather of suggestion than of proof, but the suggestion is still very decided and it is scarcely possible to exaggerate the importance of even this slender clue.

In stating the problem of Species at the beginning of this inquiry it was said that the forms of living things, as we know them, consti-

tute a discontinuous series, and it is with the origin of the Discontinuity of the series that the solution of the main problem is largely concerned. Now the evidence of Discontinuous Variation suggests that organisms may vary abruptly from the definite form of the type to a form of variety which has also in some measure the character of definiteness. Is it not then possible that the Discontinuity of Species may be a consequence and expression of the Discontinuity of Variation? To declare at the present time that this is so would be wholly premature, but the suggestion that it is so is strong, and as a possible light on the whole subject should certainly be considered.

In view of such a possible solution of one of the chief parts of the problem of Species it will be well to point out a line of inquiry which must in that event be pursued. If it can be shown that the Discontinuity of Species depends on the Discontinuity of Variation, we shall then have to consider the causes of the Discontinuity of Variation.

Upon the received hypothesis it is supposed that Variation is continuous and that the Discontinuity of Species results from the operation of Selection. For reasons given above (pp. 234 and 235) there is an almost fatal objection in the way of this belief, and it cannot be supposed both that all Variation is continuous and also that the Discontinuity of Species is the result of Selection. With evidence of the Discontinuity of Variation this difficulty would be removed.

It will be noted also that it is manifestly impossible to suppose that the perfection of a variety, discontinuously and suddenly occurring, is the result of Selection. No doubt it is conceivable that a race of tulips having their floral parts in multiples of four might be raised by Selection from a specimen having this character, but it is not possible that the perfection of the nascent variety can have been gradually built up by Selection, for it is, in its very beginning, perfect and symmetrical. And if it may be seen thus clearly that the perfection and Symmetry of a variety is not the work of Selection, this fact raises a serious doubt that perhaps the similar perfection and Symmetry of the type did not owe its origin to Selection either. This consideration of course touches only the part that Selection may have played in the first building up of the type and does not affect the view that the perpetuation of the type once constituted may have been achieved by Selection.

But if the perfection and definiteness of the type is not due to Selection but to the physical limitations under which Variation

proceeds, we shall hope hereafter to gain some insight into the nature of these limitations, though in the present state of zoological study the prospect of such progress is small. In the observations which follow I am conscious that the bounds of profitable speculation are perhaps exceeded, and I am aware that to many this may seem matter for blame; but there is, in my judgment, a plausibility in the views put forward, sufficient at least to entitle them to examination. They are put forward in no sense as a formulated theory, but simply as a suggestion for work. It is, besides, only in foreseeing some of the extraordinary possibilities that lie ahead in the Study of Variation, that the great value of this method can be understood.

It has been seen that Variations may be either Meristic or Substantive, and that in each group discontinuous and definite Variations may occur by steps which may be integral or total. We are now seeking the factors which determine this totality and define the forms assumed in Variation. In this attempt we may, by arbitrarily confining our first notice to very simple cases, recognise at least two distinct factors which may possibly be concerned in this determination. Of these the first relates to Meristic Variation and the second to Substantive Variation.

1. *Possible nature of the Discontinuity of Meristic Variation*

Looking at simple cases of Meristic Variation, such as that of the tulip or of *Aurelia*, or of the cockroach tarsus, there is, I think, a fair suggestion that the definiteness of these Variations is determined *mechanically*, and that the patterns into which the tissues of animals are divided represent positions in which the forces that effect the division are in equilibrium. On this view, the lines or planes of division would be regarded as lines or planes at right angles to the directions of the dividing forces; and in the lines of Meristic Division we are perhaps actually presented with a map of the lines of those forces of attraction and repulsion which determine the number and positions of the repeated parts, and from which Symmetry results. If the Symmetry of a living body were thus recognised as of the same nature as that of any symmetrical system of mechanical forces, the definiteness of the symmetry in Meristic Variation would call for no special remark, and the perfection of the symmetry of a tulip with its parts divided into four, though occurring suddenly as a "sport," would be recognised as in nowise more singular than the

symmetry of the type. Both alike would then be seen to owe their perfection to mechanical conditions and not to Selection or to any other gradual process. If reason for adopting such a view of the physics of Division should appear, the frequency with which in any given form a particular pattern of Division or of Symmetry recurs would be found to be determined by and to be a measure of the stability of the forces of Division when disposed in that particular pattern. It will of course be understood that in these remarks no suggestion is offered as to the causes which determine whether a tissue shall divide into four or into three, but merely as to the conditions of perfection of the division in either case. It will also be clear that though the symmetry of a flower or of any other tissue depends also on symmetrical growth, it is primarily dependent on the symmetry of its primary divisions, upon which symmetrical growth and secondary symmetrical divisions follow.

It would be interesting and I believe profitable to examine somewhat further the curiously close analogy between the symmetry of bodily Division and that of certain mechanical systems by which close imitations both of linear and of radial segmentation can be produced; and though to some this might seem over-daring, the possibility that the mechanics of bodily Division are in their visible form of an unsuspected simplicity is so far-reaching that it would be well to use any means which may lead others to explore it.

And even if at last this suggestion shall be found to have in it no other element of truth, it would still be of use as a forcible presentation of the fact, which when realised can hardly be doubted, that among the factors which combine to form a living body, the forces of Division may be distinguished as in their manifestations separable from the rest and forming a definite group. For already (Section v) it has been pointed out that the patterns of Division or Merism may be changed, while the Substance of the tissues presents to our senses no difference. The recognition of this essential distinctness of the Meristic forces will, I believe, be found to supply the base from which the mechanics of growth will hereafter be attacked.

The problems of Morphology will thus determine themselves into problems in the physiology of Division, which must be recognised together with Nutrition, Respiration and Metabolism, as a fundamental property of living protoplasm.

To sum up: there is a possibility that Meristic Division may be a strictly *mechanical* phenomenon, and that the perfection and

Symmetry of the process, whether in type or in variety, may be an expression of the fact that the forms of the type or of the variety represent positions in which the forces of Division are in a condition of Mechanical Stability.

2. *Possible nature of the Discontinuity of Substantive Variation*

Passing from the phenomena of Division and arrangement to those of constitution or substance we are, as has been said, again presented with the phenomenon of discontinuous or total Variation, and we must seek for causes which may perhaps govern and limit this totality, and in obedience to which the Variation is thus definite. Now as in the case of Meristic Variation, by arbitrarily limiting the examination to those cases which seem the simplest, it appears that there is at least an analogy between them and certain mechanical phenomena, so by similarly restricting ourselves to very simple cases there will be seen to be a similar analogy between the discontinuity of some Substantive Variations and that of *chemical* discontinuity. It is on the whole not unreasonable to expect that the definiteness of at least some Substantive Variations depends ultimately on the discontinuity of chemical affinities. To take but one instance, that of colour, we are familiar with the fact that the colours of many organic substances undergo definite changes when chemically acted on by reagents, and it is not suggested that the definiteness and discontinuity of the various colours assumed is dependent on anything but the definiteness of the chemical changes undergone. The changes of litmus and many vegetable blues to red on treatment with acids, of many vegetable yellows to brown on treatment with alkalies, the colours of the series of bodies produced by the progressive oxidation of biliverdin are familiar examples of such definite colour-variations.

With facts of this kind in view, the conclusion is almost forced on us that the definiteness of colour-variation is a consequence of the definiteness of the chemical changes undergone. No one doubts that the orange colouring matter of the variety of the Iceland poppy (*P. nudicaule*) is a chemical derivative from the yellow colouring matter of the type. It is not questioned that in such cases a definite alteration in the chemical conditions in which the pigment is produced determines whether the flower shall be orange or yellow; and I think it is reasonable to expect that the frequency with which the flowers are either yellow or orange as compared with the rarity of the intermediate shades is an expression of the fact that the yellow and

orange forms of the colouring matter have a greater chemical stability than the intermediate forms of the pigment, or than a mixture of the two pigments. If then it should happen, as we may fairly suppose it might, that the orange form were to be selected and established as a race, it would owe the definiteness of its orange colour and the precision of its tint, not to the precision with which Selection had chosen this particular tint, but to the chemical discontinuity of which the originally discontinuous Variation was the expression.

To pass from the case of a sport to that of Species, it is well known that of the many S. African butterflies of the genus *Euchloe* (= *Anthocharis*, Orange-tips), some have the apices or tips of the fore-wings orange-red (for example, *E. danæ*), while in others they are purple (for example, *E. ione*). Upon the view that the transition from orange to purple, or *vice versâ*, had been continuously effected by the successive Selection of minute variations, we are met by all the difficulties we know so well. Why is purple a good colour for this creature? If purple is a good colour and red is a good colour, how did it happen that at some time or other all the intermediate shades were also good enough to have been selected? and so on. These and all the cognate difficulties are opened up at once, and though they have been met in the fashion we know, they have scarcely been overcome. But at the outset this view assumes that every intermediate may exist and has existed, an assumption which is gratuitous and hardly in accordance with the known fact that chemical processes are frequently discontinuous. When besides this it is known that Variation *may* be discontinuous, I submit that it is easier to suppose that the change from red to purple was from the first complete, and that the choice offered to Selection was between red and purple; and that the tints of the purple and of the red were determined by the chemical properties of the body to which the colour is due. This case is a particularly interesting one in the light of the fact that, as Mr F. G. Hopkins has lately shown me, this purple colour, dissolved in hot water, leaves on evaporation a substance which gives the murexide reaction and cannot as yet be distinguished from the substance similarly derived from the orange or yellow colouring matters of Pieridæ in general. As was stated above, Mr Hopkins has shown that these yellows are acids, allied to mycomelic acid, a derivative of uric acid, and therefore of the nature of excretory products. Whether the purple body is related to the yellow or to the orange as a salt is to an acid, or otherwise, cannot yet be affirmed; but if the difference

between them is a chemical difference, which can hardly be doubted, there is at least a presumption that the discontinuity of these colours in the several species is an expression of the discontinuity of the chemical properties of this body. The possibility that from such bodies a series of substances might perhaps by suitable means be prepared in such a way as to represent many or even all intermediate shades, does not greatly affect the suggestion made; for even in such series it is almost certain that points of comparative stability would occur, and Discontinuity would thus be introduced.

The case of Colour has been taken in illustration because it is the simplest and most intelligible example of the possibility that the Discontinuity of some Substantive Variations is determined by the Discontinuity of the chemical processes by which the structures are produced. It is true that perhaps no species has been rightly differentiated by colour alone, but colour is still one of the many characters which go to the distinguishing of a species, and it is precisely one of the characters whose significance and delimitation by Natural Selection is most obscure. Moreover by the fact that in the case of these yellow and red Pieridæ the colours are of an excretory nature, we are reminded that Variation in colour may be an index of serious changes in the chemical economy of the body, and that when an animal is said to be selected because it is red or because it is purple, the real source of its superiority may be not its red colour or its purple colour, but other bodily conditions of which these colours are merely symptoms. By those who have attempted to reconcile the phenomena of Colour with the hypothesis of Natural Selection this fact is too often overlooked.

But though it may reasonably be supposed that much of the Discontinuity of Variation and some of the Discontinuity of Species arise through discontinuous transition from one state of mechanical or chemical stability to another state of stability, there nevertheless remain large classes of Discontinuous Variations, and of Specific Differences still more, whose Discontinuity bears no close analogy with these. To these phenomena inorganic Nature offers no parallel. We may see that they are discontinuous and that their course is in some way controlled, but as to the nature of this control we can make no guess.

Though the resemblance may be misleading, it is nevertheless true that in *living* Nature there are other phenomena, those of disease,

which present a Discontinuity closely comparable with that of many Variations. In problems of disease we meet again the same problem which we meet in Variation, namely, changes which may be complete or specific, though occurring so suddenly as to exclude the hypothesis that Selection has been the limiting cause. All this is familiar to everyone who has considered the problem of Species.

For though, like discontinuous Variations, the manifestations of specific disease are not always identical, but differ in intensity and degree, varying about a normal form, still these manifestations may be specific in the sense in which the term is used with reference to the characters of Species. If we exclude those diseases whose specific characters are now known to be the result of the invasion of specific organisms, there still remain very many which are known and recognised by definite and specific symptoms produced in the body, though there is as yet no evidence that they are due to specific organisms. [Of course if it were shown that these diseases also result from the action of specific organisms, they then only present to us again the original problem of Species; for if the definiteness, or Species, of a disease is due to the definiteness, or Species, of the micro-organism which causes it, the cause of that definiteness of the micro-organism remains to be sought, and we are simply left with a particular case of the general problem of Species.] But in the meantime we can see that the manifestations are specific; and while we do not know that they result from causes themselves specific, the nature of the control in obedience to which they are specific is unknown.

The parallel between disease and Variation may be misleading, but this much at least may fairly be learned from it: that the system of an organised being is such that the result of its disturbance may be specific. And in the end it may well be that the problem of Species will be solved by the study of pathology; for the likeness between Variation and disease goes far to support the view which Virchow has forcibly expressed, that "every deviation from the type of the parent animal must have its foundation on a pathological accident[1]."

[1] R. Virchow, *Journal of Pathology*, I, 1892, p. 12.

SECTION XIV

Some current conceptions of Biology in view of the facts of Variation

Enough has now been said to explain the aim of the Study of Variation, and to show the propriety of the choice of the facts of Meristic Variation as a point of departure for that study. Before leaving this preliminary consideration, reference to some cognate subjects must be made.

It has been shown that in view of the facts of Variation, some conceptions of modern Morphology must be modified, while others must be abandoned. With the recognition of the significance of the phenomena of Variation, other conceptions of biology will undergo like modifications. As to some of these a few words are now required if only to explain methods adopted in this work.

1. *Heredity.*

It has been the custom of those who have treated the subject of Evolution to speak of "Heredity" and "Variation" as two antagonistic principles; sometimes even they are spoken of as opposing "forces."

With the Study of Variation, such a description of the processes of Descent will be given up, even as a manner of speaking. In what has gone before I have as far as possible avoided any use of the terms Heredity and Inheritance. These terms, which have taken so firm a hold on science and on the popular fancy, have had a mischievous influence on the development of biological thought. They are of course metaphors from the descent of property, and were applied to organic Descent in a time when the nature of the process of reproduction was wholly misunderstood. This metaphor from the descent of property is inadequate chiefly for two reasons.

First, by emphasising the fact that the organisation of the offspring depends on material transmitted to it by its parents, the metaphor of Heredity, through an almost inevitable confusion of thought, suggests the idea that the actual body and constitution of the parent are thus in some way handed on. No one perhaps would now state the facts in this way, but something very like this material view of Descent was indeed actually developed into Darwin's Theory of Pangenesis. From this suggestion that the body of the parent is in

some sort remodelled into that of the offspring, a whole series of errors are derived. Chief among these is the assumption that Variation must necessarily be a continuous process; for with the body of the parent to start from, it is hard to conceive the occurrence of discontinuous change. Of the deadlock which has resulted from the attempt to interpret Homology on this view of Heredity, I have already spoken in Section VI.

Secondly, the metaphor of Heredity misrepresents the essential phenomenon of reproduction. In the light of modern investigations, and especially those of Weismann on the continuity of the germ-cells, it is likely that the relation of parent to offspring, if it has any analogy with the succession of property, is rather that of trustee than of testator.

Hereafter, perhaps, it may be found possible to replace this false metaphor by some more correct expression, but for our present purpose this is not yet necessary. In the first examination of the facts of Variation, I believe it is best to attempt no particular consideration of the working of Heredity. The phenomena of Variation and the *origin* of a variety must necessarily be studied first, while the question of the perpetuation of the variety properly forms a distinct subject. Whenever in the cases given observations respecting inheritance are forthcoming they will be of course mentioned. But speaking of discontinuous Variation in general, the recurrence of a Variation in offspring, either in the original form or in some modification of it, has been seen in so many cases, that we shall not go far wrong in at least assuming the possibility that it *may* reappear in the offspring. At the present moment, indeed, to this statement there is little to add. So long as systematic experiments in breeding are wanting, and so long as the attention of naturalists is limited to the study of normal forms, in this part of biology which is perhaps of greater theoretical and even practical importance than any other, there can be no progress.

2. *Reversion.*

Around the term Reversion a singular set of false ideas have gathered themselves. On the hypothesis that all perfection and completeness of form or of correlation of parts is the work of Selection it is difficult to explain the discontinuous occurrence of new forms possessing such perfection and completeness. To account for these, the hypothesis of Reversion to an ancestral form is proposed, and with some has found

favour. That this suggestion is inadmissible is shown at once by the frequent occurrence by discontinuous Variation of forms which, though equally perfect, cannot all be ancestral. In the case of *Veronica* and *Linaria*, for example, a host of symmetrical forms of the floral organs may be seen occurring suddenly as sports, and of these though any *one* may conceivably have been ancestral, the same cannot be supposed of all, for their forms are mutually exclusive. On *Veronica buxbaumii*, for instance, are many symmetrical flowers having *two* posterior petals, like those of other Scrophularineæ: these may reasonably be supposed to be ancestral, but if this supposition is made, it cannot be made again for the equally perfect forms with three petals, and the rest[1].

The hypothesis of Reversion to account for the Symmetry and perfection of modern or discontinuous Variation is made through a total misconception of the nature of Symmetry.

There is a famous passage in the *Descent of Man*, in which Darwin argues that the phenomenon of double uterus, from its perfection, must necessarily be a Reversion.

> ..."In other and rarer cases, two distinct uterine cavities are formed, each having its proper orifice and passage. No such stage is passed through during the ordinary development of the embryo, and it is difficult to believe, though perhaps not impossible, that the two simple, minute, primitive tubes could know how (if such an expression may be used) to grow into two distinct uteri, each with a well-constructed orifice and passage, and each furnished with numerous muscles, nerves, glands and vessels, if they had not formerly passed through a similar course of development, as in the case of existing marsupials. No one will pretend that so perfect a structure as the abnormal double uterus in woman could be the result of mere chance. But the principle of reversion, by which long-lost dormant structures are called back into existence, might serve as the guide for the full development of the organ, even after the lapse of an enormous interval of time[2]." *Descent of Man*, vol. I, pp. 123 and 124.

[1] For a full account of such facts, see a paper by Miss A. Bateson and myself "On Variations in Floral Symmetry," *Journ. Linn. Soc.* XXVIII, p. 386 [p. 126 *supra*].

[2] This extraordinary passage is scarcely worthy of Darwin's penetration. If read in the original connection it will seem strange that it should have been allowed to stand. For in a note to these reflections on Reversion (*Descent*, I, p. 125) Darwin refers to and withdraws his previously expressed view that supernumerary digits and mammæ were to be regarded as reversions. This view had been based on the perfection and symmetry with which these variations reproduce the structure of putative ancestors. It was withdrawn because Gegenbaur had shown that polydactyle limbs

This kind of reasoning has been used by others again and again. It is of course quite inadmissible; for by identical reasoning from the perfect symmetry of double monsters, of the single eye of the Cyclopian monster, and so on, it might be shown that Man is descended from a primitive double vertebrate, from a one-eyed Cyclops and the like. For other reasons it is likely enough that double uterus was a primitive form; but the perfection and symmetry of the modern Variation to this form is neither proof nor indication of such an origin. Such a belief arises from want of knowledge of the facts of Meristic Variation, and is founded on a wrong conception of the nature of symmetry and of the mechanics of Division. The study of Variation shows that it is a common occurrence for a part which stands in the middle line of a bilaterally symmetrical animal to divide into two parts, each being an optical image of the other: and that conversely, parts which normally are double, standing as optical images of each other on either side of such a middle line may be compounded together in the middle line forming a single, symmetrical organ.

It would probably help the science of Biology if the word "Reversion" and the ideas which it denotes were wholly dropped, at all events until Variation has been studied much more fully than it has yet been.

In the light of what we now know of the process of reproduction the phrase is almost meaningless. We suppose that a certain stock gives off a number of individuals which vary about a normal; and that after having given them off, it begins to give off individuals varying about another normal. We want to say that among these it now and then gives off one which approaches the first normal, that shooting at the new mark it now and then hits the old one. But all that we know is that now and then it shoots wide and hits *another* mark, and we assume from this that it would not have hit it if it had not aimed at it in a bygone age. To apply this to any other matter would be absurd. We might as well say that a bubble would not be round if the air in it had not learned the trick of roundness by having been in a bubble before: that if in a bag after pulling out a lot of white balls I find a totally red one, this proves that the bag must have once been full of

often bear no resemblance to those of possible ancestors, and because extra mammæ may not only occur symmetrically and in places where they are normal in other forms, but also in several quite anomalous situations. In the light of this knowledge it is strange that Darwin should have continued to regard the perfection and symmetry of a Variation as evidence that it is a Reversion.

red balls, or that the white ones must all have been red in the past.

Besides the logical absurdity on which this use of the theory of Reversion rests, the application of it to the facts of Variation breaks down again and again. I have already mentioned some cases of this, but there are many others of a different class. For instance, it will be shown that the percentage of extra molars in the Anthropoid Apes is almost the highest reached among mammals. On the usual interpretation, such teeth are due to Reversion to an ancestral condition with four molars, and on less evidence it has been argued that a form frequently showing such "Reversion" is older than those which do not. From this reasoning it should follow that the Anthropoids are the most primitive form, at least of monkeys. It is surely time that these brilliant and facile deductions were no more made in the name of science.

3. *Causes of Variation.*

Inquiry into the causes of Variation is as yet, in my judgment, premature.

4. *The Variability of "useless" Structures.*

The often-repeated statement that "useless" parts are especially variable finds little support in the facts of Variation, except in as far as it is a misrepresentation of another principle. The examples taken to support this statement are commonly organs standing at the end of a Meristic Series of parts, in which there is a progression or increase of size and degree of development, starting from a small terminal member. In such cases, as that of the last rib in Man, and several other animals, the wisdom-teeth of Man, etc., it is quite true that in the terminal member Variation is more noticeable than it is in the other members. This is, I believe, a consequence of the mechanics of Division, and has no connection with the fact that the functions of such terminal parts are often trifling. Upon this subject something will be said later on, but perhaps a rough illustration may make the meaning more clear at this stage. If a spindle-shaped loaf of bread, such as a "twist," be divided with three cuts taken at equal distances, in such a way that the two end pieces are much shorter than the middle ones, to a child who gets one of the two large middle pieces the contour-curves of the loaf will not matter so much; but to a child who gets one of the small end bits, a very slight alteration in the curves of the loaf will make the difference between a fair-sized bit and almost

nothing, a difference which the child will perceive much more readily than the complementary difference in the large pieces will be seen by the others. An error in some measure comparable with this is probably at the bottom of the statement that useless parts are variable, but of course there are many examples, as the pinna of the human ear, which are of a different nature. It is unnecessary to say that for any such case in which a part, apparently useless, is variable, another can be produced in which some capital organ is also variable; and conversely, that for any case of a capital organ which is little subject to Variation can be produced a case of an organ, which, though trifling and seemingly "useless," is equally constant. With a knowledge of the facts of Variation, all these trite generalities will be forgotten.

5. *Adaptation.*

In examining cases of Variation, I have not thought it necessary to speculate on the usefulness or harmfulness of the Variations described. For reasons given in Section II, such speculation, whether applied to normal structures or to Variation, is barren and profitless. If any one is curious on these questions of Adaptation, he may easily thus exercise his imagination. In any case of Variation there are a hundred ways in which it may be beneficial or detrimental. For instance, if the "hairy" variety of the moorhen became established on an island, as many strange varieties have been, I do not doubt that ingenious persons would invite us to see how the hairiness fitted the bird in some special way for life in that island in particular. Their contention would be hard to deny, for on this class of speculation the only limitations are those of the ingenuity of the author. While the only test of utility is the success of the organism, even this does not indicate the utility of one part of the economy, but rather the nett fitness of the whole.

6. *Natural Selection.*

In the view of the phenomena of Variation here outlined, there is nothing which is in any way opposed to the theory of the Origin of Species "by means of Natural Selection, or the preservation of favoured races in the struggle for life." But by a full and unwavering belief in the doctrine as originally expressed, we shall in no way be committed to representations of that doctrine made by those who have come after. A very brief study of the facts will suffice to gainsay such statements as, for example, that of Claus, that "it is only *natural*

selection which accumulates those alterations, so that they become appreciable to us and constitute a variation which is evident to our senses[1]." For the crude belief that living beings are plastic conglomerates of miscellaneous attributes, and that order of form or Symmetry have been impressed upon this medley by Selection alone; and that by Variation any of these attributes may be subtracted or any other attribute added in indefinite proportion, is a fancy which the Study of Variation does not support.

Here this Introduction must end. As a sketch of a part of the phenomena of Variation, it has no value except in so far as it may lead some to study those phenomena. That the study of Variation is the proper field for the development of biology there can be no doubt. It is scarcely too much to say that the study of Variation bears to the science of Evolution a relation somewhat comparable with that which the study of affinities and reactions bears to the science of chemistry: for we might almost as well seek for the origin of chemical bodies by the comparative study of crystallography, as for the origin of living bodies by a comparative study of normal forms.

[1] *Text-book of Zoology*, Sedgwick and Heathcote's English translation, vol. I, p. 148. In the original the passage runs: "*erst die natürliche Zuchtwahl häuft und verstärkt jene Abweichungen in dem Masse dass sie für uns wahrnehmbar werden* und eine in die Augen fallende Variation bewirken." C. Claus, *Lehrb. d. Zool.* ed. 2, 1883, p. 127, and *Grundzüge der Zoologie*, 1880, Bd. I, p. 90. The italics are in the original.

ON TWO CASES OF COLOUR-VARIATION IN FLAT-FISHES ILLUSTRATING PRINCIPLES OF SYMMETRY

[*Proceedings of the Zoological Society*, March 6, 1894]

(With Plate V)

THE two cases of Variation here described are both examples of abnormal deposit of pigment in the skin of the normally unpigmented or "blind" side of flat-fishes. The two cases are unlike each other, but both are remarkable illustrations of the ways in which the phenomenon of Symmetry may be manifested and may contribute to the production of a definite result in Variation that is presumably sporadic.

The first specimen is a small brill (*Rhombus lævis*), kindly sent to me by Mr Matthias Dunn, of Mevagissey, Cornwall. It is $9\frac{3}{4}$ inches long, and $6\frac{1}{2}$ inches wide in the widest part. The dorsal fin, the eyes, and other parts are normal in form and position. The only abnormality seen consists in the presence of a row of five spots of colour along the dorsal border of the body on the blind side, and of another row of three spots along the ventral border on the same side. The spots are on the body, central to the dorsal and anal fins, which are both of normal colour. The interest of the case lies in the remarkable symmetry with which the spots are distributed with reference to the longitudinal axis of the body. On reference to the plate (Pl. V) it will be seen that each of the three ventral spots stands at very nearly the same transverse level as one of the spots of the dorsal series. The two anterior spots of the dorsal series have no representatives in the ventral series. This appearance of symmetry, so striking to the eye, is upon examination found to be an expression of the fact that the ordinal positions of the neural spines crossing the centres of the spots of the dorsal row are, if reckoned from behind forwards, almost exactly the same as those of the hæmal spines crossing the centres of the ventral spots.

The particulars are as follows: The centre of the most posterior dorsal spot stands almost exactly over the neural spine of the 11th fin-ray, reckoning from behind. The centre of the next spot is upon that of the 26th fin-ray reckoned from behind; that of the next is on the 42nd.

Of the ventral spots the centre of the most posterior is on the hæmal spine of the 11th fin-ray from behind; that of the next is on

the 24th, and that of the most anterior is on the 40th. It will be seen that the numbers in the two rows closely correspond.

Continuing the dorsal series there is a spot on the neural spine of the 52nd fin-ray, another very minute and faint spot over the 63rd. In front of this there are 16 more fin-rays.

The whole number of fin-rays in the dorsal fin is 79, and in the anal fin 58.

On detailed examination it may be seen that the spots are not wholly shapeless blotches of colour, but that some of them consist of several irregular zones of colours. Each of these spots is thus a somewhat indefinite ocellar mark. The spots *dd*, *vc*, and *vb* have each a minute centre of light colour, which is chiefly due to the presence of a whitish scale in the middle of the spot. This light colour is not altogether confined to the one scale, but spreads a little on to the edges of the adjacent scales. The spot *db* has *two* of these small whitish centres. The spot *dc* alone of the five chief spots has no light centre. Around the centre of each spot are scales of a brown tint bearing specks of very dark pigment. These deeply pigmented scales form a zone about four rows deep in the case of the larger spots. Outside this is an irregular zone of fine pigment-granules giving a neutral tint. Beyond this again there was in the case of spots *dd*, *dc*, *db*, and *vc* a vague and imperfect band of silvering, forming a border to the proximal limbs of the spots.

It is thus seen that the colours of the dorsal and ventral borders have, so far as the last three spots are concerned, varied *similarly and simultaneously*, producing a result that is nearly symmetrical about the horizontal axis. This phenomenon is precisely comparable with the much more common phenomenon of similar and simultaneous Variation of the right and left sides of a bilaterally symmetrical body. It is to be remembered that in many fishes, and especially in flat-fishes, there is an imperfect relation of bilateral symmetry subsisting between the parts dorsal and ventral to the horizontal median plane. This symmetry is generally manifested both in form and colour, and is an indication that at some time these parts have undergone similar Variation. The present example illustrates the principle that parts, which in the normal are in symmetry with each other, are related to each other in such a way that they may undergo similar Variations *simultaneously*. Upon the deductions from this principle I have dwelt elsewhere.

Several forms of abnormal pigmentation upon the "blind" side

of flat-fishes are of course familiar, but of the particular Variation here seen I have met with no other case. In a recent paper, however, Cunningham[1] makes allusion to cases apparently of this nature, saying that they are frequent in the brill. So far as I know, the occurrence is not mentioned by the other authors who have treated of the colour-variations of flat-fishes.

The other specimen is one to which I lately made reference in writing on the subject of pigmentation in the blind sides of flat-fishes[2]. The description that I gave was very brief and not quite correct, and I take this opportunity of amplifying and correcting it. It may appropriately be considered here inasmuch as it also illustrates the influence of Symmetry in determining the manner of occurrence of Variation, though in a way different from that seen in the brill described above. The fish is a plaice (*Pleuronectes platessa*), also received from Mr Dunn. Its fins, eyes, etc., were normal. The posterior half of the "blind" side was fully pigmented, the pigmented area being sharply limited at a sinuous line slightly behind the level of greatest width. This pigmented area was of the same colour as the skin of the upper surface, and, like it, bore spots of a full orange colour. Of these spots there were, in all, thirteen—eight being on the body, three on the dorsal fin, and two on the anal. The interest of the case lies in the fact that by passing pins vertically through the body it was proved that the centres of *nine* of these spots coincided exactly with the centres of spots on the upper side. Four of these coincident spots were ventral to the lateral line, two being on the body and two on the anal fin. One large spot was upon the lateral line. Three were upon the dorsal fin, and one, a large spot, was also upon the body, just anterior to the base of the caudal fin. There was one spot over the muscles of the dorsal fin which very nearly corresponded with a similar spot on the upper side.

In the same region were two more spots on the lower side that were each represented on the upper side, but they were not in correspondence with their representatives, but *alternated* with them. *One* large spot on the lower side, ventral to the lateral line, anterior to the base of the caudal fin, was wholly unrepresented on the upper side.

The manner of occurrence of this Variation proves that, though in

[1] Cunningham, J. T., *Phil. Trans.* 1894, CLXXXIV, B, p. 807.

[2] *Materials for the Study of Variation*, 1894, p. 467. The account there given contains a misprint. For "of these, 13 spots on body and fins coincided" read "of these 13 spots on body and fins, 9 coincided."

a normal flat-fish there is a great dissimilarity between the coloration of the upper and lower sides, yet, when the lower side assumes the characters of the upper, it may do so in such a way as to produce a result which is approximately bilaterally symmetrical. Of the general significance of this phenomenon I have spoken in the place referred to.

It should be observed that this specimen does not at all precisely conform to the principle of Symmetry illustrated by the brill described above. There was nevertheless in it also an imperfect correspondence between the distributions of the spots upon the areas dorsal and ventral to the median axis. Asymmetry, however, was exhibited in the presence of one spot on the dorsal fin, and of one spot over the dorsal neural spines, that were not represented in the area ventral to the lateral line.

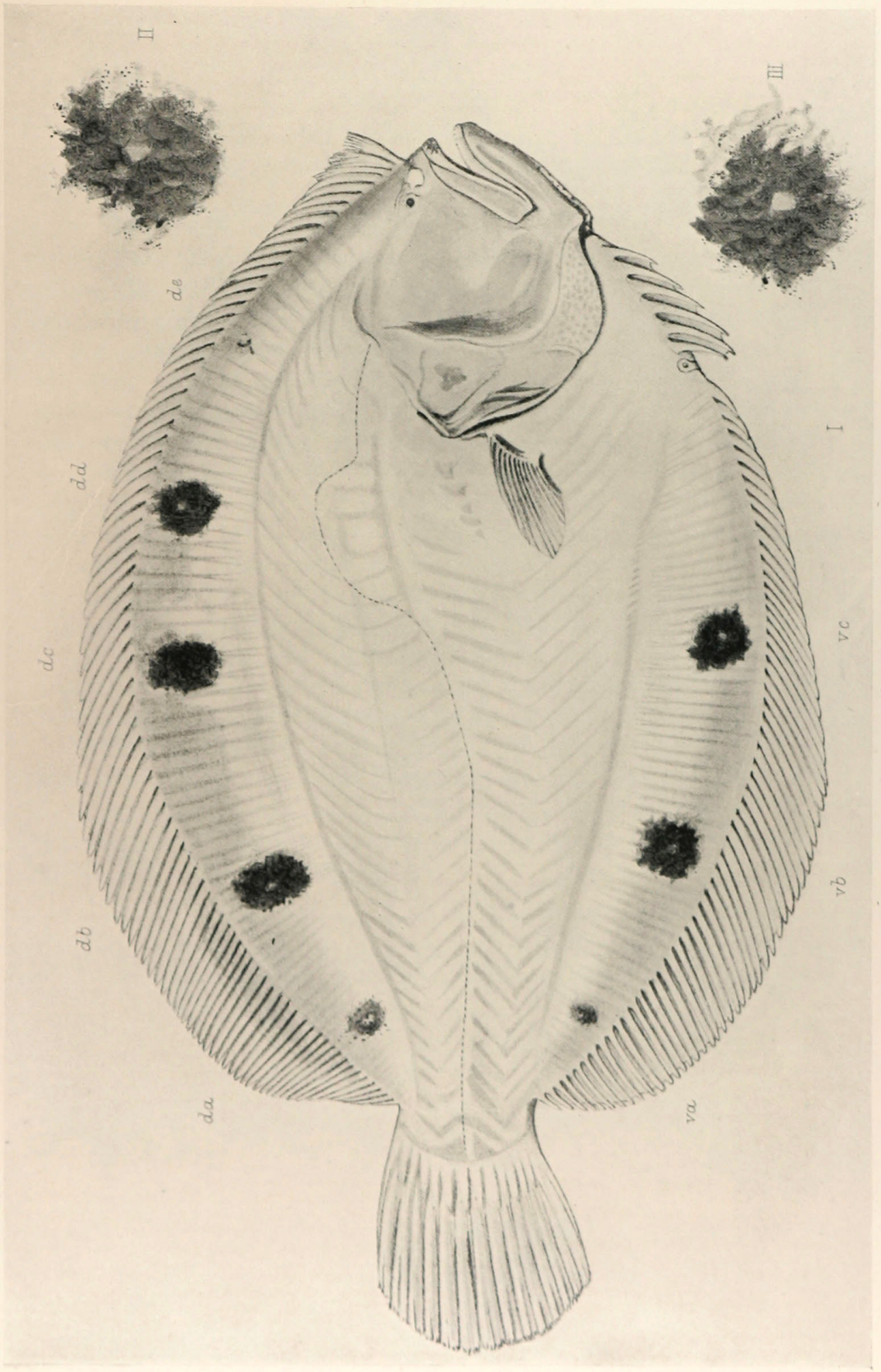
I am not aware that flat-fishes having pigment upon their "blind" sides have before been examined with a view to this question; and owing to the importance of the matter with regard to the defining of the principles of Symmetry, such an examination should be made in all cases where the presence of definite spots or marks makes the determination possible.

In contrast with these cases of symmetrical Variation were exhibited photographs of a sample of flounders (*Platessa flesus*) from the shallow water near Bournemouth. In this locality there is a high percentage of specimens having pigment on the "blind" sides. Of a sample of 32 all but three were to some extent spotted with pigment. In five this spotting was so great as to give them a piebald appearance, and of these one was over the greater part of the "blind" side of a full brown colour. No regularity whatever could be detected in the distribution of the pigment. This sample represented the normal condition of the flounders of the locality, and had not been in any way selected.

Explanation of Plate V[1]

Fig. 1. View of the "blind" side of abnormal specimen of *Rhombus lævis*. ⅔ nat. size.
Fig. 2. Enlarged view of the spot *dd*.
Fig. 3. Enlarged view of the spot *vb*.

[1] [This plate has been reproduced in black and white from the original tinted lithographic one. Ed.]



Variety of *Rhombus lævis*

NOTE IN CORRECTION OF A PAPER ON COLOUR-VARIATION IN FLAT-FISHES

[*Proceedings of the Zoological Society*, December 17, 1895]

In the *Proceedings* of this Society, 1894, p. 246, I published an account of an abnormal brill (*Rhombus lævis*) having a series of dark spots along the dorsal and ventral borders of the body on the "blind" side. In commenting on this case, stress was laid on the fact that the corresponding parts of the dorsal and ventral borders had thus varied similarly and simultaneously. At the time I was under the impression that the Variation observed was a sudden appearance of a character not otherwise met with in flat-fishes; but since the publication of the paper Professor W. C. McIntosh has informed me that flat-fishes of some species in the ordinary course of development, while swimming on edge, go through a stage in which they are marked on both sides with a row of dorsal and ventral spots placed just as in my specimen. He has referred me to his paper in *Proc. Roy. Inst.* 1889, XII, p. 396, where examples of such larval fishes are figured. I am further indebted to Prof. McIntosh for a specimen showing this condition, and similar specimens were also shown to me by Mr E. W. L. Holt.

My case of Variation is therefore an example of a persistence of larval coloration, and not of the appearance of a new character. It is consequently much less important than I imagined, though the comment respecting the similarity and simultaneity of the Variation of the two borders still applies.

THE ORIGIN OF THE CULTIVATED CINERARIA

[*Nature*, LI, 1895]

RETURNING from abroad, I have just seen Mr Dyer's letter in *Nature*, March 14. Of the matters there treated I ask leave now to deal with one only, that numbered (18). This is a point of fact—the origin of the cultivated Cineraria. At a meeting of the Royal Society, on Feb. 28, Mr Dyer exhibited a specimen of *Cineraria cruenta* from the Canaries, side by side with a plant of the common cultivated form. With the object of minimising the value of "sports" in evolution, this exhibition was made to illustrate what can be done "by the gradual accumulation of small variations." Mr Dyer stated, if I rightly understood him, first, that of the two forms exhibited, the one had been produced from the other; secondly, that, as far as is known, this process of evolution had been accomplished by the gradual accumulation of small Variations, and not by the selection of "sports" or seedlings presenting notable and striking Variations. That in the case of a plant much modified by gardeners in recent times such a history would be highly unusual, Mr Dyer will, I think, admit.

Doubting this account, and searching records of the early culture of the Cineraria for my own satisfaction, I found a good deal of miscellaneous information on the subject. This history is not yet quite complete; but as Mr Dyer's account has now appeared in print, the following notes may be of use.

In the ordinary manuals (*e.g.* Burbidge, *Propagation*, etc., 1877, p. 150) it is said that the florists' Cinerarias are *hybrids*, obtained by crossing and recrossing several species of *Cineraria* (or more strictly *Senecio*). As to the exact parentage, there is not entire certainty. Burbidge gives *C. cruenta*, *aurita* and *lanata* as the parents. Other writers mention *C. maderensis*, *multiflora*, *tussilaginis* and *populifolia* as having contributed (cp. *Journ. d'hort. Gand*, II, 1846, p. 231). General statements of a like nature are made by many. For the account given by Mr Dyer I find no authority except one, an article by Rolfe (*Gard. Chron.* 1888 (I), p. 653). Here *C. cruenta* is given as the sole parent, and a figure of this species raised at Kew, from wild seed, is shown beside two extreme flowers of the modern type. Excepting this statement, it seems agreed that the species originally

concerned are at least four: *cruenta*, *aurita*, *populifolia* and *lanata*. The first three have comparatively small flowers in corymbs or cymes. Those of *cruenta*, introduced from Canary by Masson to Kew in 1777, are purple. This species was originally described from Teneriffe by L'Héritier, *Sert. Angl.* 1788, Pl. 33, and is figured *Bot. Mag.* t. 406, and elsewhere. The lower surface of the leaves is purplish. The petioles have auricular expansions. *C. aurita*, sent to Kew from Madeira 1790, figured by L'Héritier, Pl. 31, and *Bot. Mag.* t. 1786, is a somewhat different plant, of more slender habit, said to be more akin to *populifolia*. The flowers are purple. Ray-florets few and irregular. Petiolar expansions variable, mostly much smaller than in *cruenta*. *C. populifolia*, L'Hér., Canaries, brought by Masson from Teneriffe 1780, is a form with yellow flowers. *C. lanata*, L'Hér., Pl. 30, and *Bot. Mag.* t. 53, is a plant very different from any of the others. It bears large purple flowers, some two inches across, only one to a peduncle. The leaves are cordate-subrotund and septangular, and woolly underneath. L'Héritier gives it as from Teneriffe. The *Bot. Mag.* wrongly says it had been introduced from Africa (perhaps confusing with *lanosa*, DC. = *lanata* Thunb.). The large flowers and peculiar leaves at once distinguish this species from the rest.

It should be added that *populifolia* in its native state showed considerable diversity in the forms of its leaves, three varieties being specified by de Candolle, *Prodr.* VI, p. 409. A natural variety of the same species with *white* flowers was brought from Teneriffe by Webb. This is the *β. leucanthus* DC. It is figured in *Flor. Cab.* I, p. 73, from a specimen grown in Birmingham Botanic Garden. As to these species, references to further information may be found in de Candolle, *Prodr.*, and in Webb, *Phytogr. Canar.*, etc.

These four species with others were at the beginning of this century pretty generally distributed in greenhouses in England, France, and Germany. They are enumerated in most of the horticultural treatises of the period, with directions for their propagation. *C. lanata* was thought the best. "It far exceeds all others cultivated here in the beauty of its flowers....It is valuable on account of its hardiness, its readiness to flower, and the facility with which it may be propagated." Rees, *Cycl. of Arts and Sci.* VIII, 1819. Others speak to like effect.

The first mention I have found of any distinct garden form is that of Willdenow, who in *Enum. Pl. Berol.* 1809, p. 893, gives *C. hybrida*, saying that this plant is grown in gardens under the name of *C.*

cruenta, but that it in reality differs much from the latter, and has flowers almost like those of *C. lanata*.

Between 1820 and 1830 definite efforts were made to improve the Cineraria. The first published is that of Bouché. Writing in the *Verh. zur Beförd. d. Gartenbauer, Berl.* I, 1824, p. 139, he says that having grown *C. lanata* L'Hér., *C. cruenta* L'Hér., and *C. hybrida* Willd., and noticed that the first two seeded freely, it occurred to him to try to raise varieties or sports (*Spielarten*), and at the same time to test the distinctness of these species. His seedlings flowered in the following year. Those from *C. cruenta* had the flowers rose-red, except one which was quite white, the flowers of the parent being dark red. The seedlings from *C. hybrida* varied so much that they might be mistaken for separate species. His words are as follows: "Unter denen von der Cin. hybrida zeichneten sich besonders fünf Abänderungen aus, welche eine ganz eigenthümliches Ansehen bekommen haben, und leicht von Botanikern, denen die Entstehungsart derselben nicht bekannt ist, für neue, noch unbeschriebene Arten dieser Gattung gehalten werden könnten." His description follows. In particular, the foliage had varied greatly from the parent form, somewhat resembling *lanata*, suggesting to Bouché that there may have been hybridisation with that species.

About the same time Mr Drummond, then Curator of the Botanic Garden, Cork, published a paper in the *Gard. Mag.* II, 1827, p. 153. He says that Cinerarias are favourites with him, especially *cruenta*, "for besides the great beauty and variety in the flowers, its fine purple blossoms form a beautiful contrast, etc." "We seldom see it cultivated to the extent it merits. The following account of the method I have followed for some years of growing this plant...may turn the attention of your readers to the cultivation of the *C. cruenta*, the effects of which *will, in all probability, be the production of fine double and single varieties of different colours, as it sports greatly from seed.* [Italics are mine.] Except in cases when it becomes desirable to preserve any particular variety for its superior beauty, I prefer raising the *C. cruenta* from seeds....Care should be taken to select the finest varieties, and those that produce the largest and finest heads or corymbs of flowers." "The other greenhouse species I cultivate are *lanata, hybrida, geifolia* and *amelloides*. These I increase by cuttings, etc."

It happens that in the same year (1827) of the *Gard. Mag.* p. 446, there is a reference to Bouché's paper. Not improbably Drummond

may have read the latter, for in Loudon's *Ladies' Mag. of Gard.* 1842, p. 111, I find this passage: "Most of the purple Cinerarias are varieties or hybrids of *C. cruenta*....It was long a favourite in greenhouses, and was generally propagated by dividing the roots; but about 1827, Mr Drummond, Curator of the Botanic Garden in Cork, having raised it from seed, and found the seedlings vary considerably, conceived the idea of hybridising it with *C. lanata*, *C. geifolia* and *C. amelloides*. The trials, however, with *C. geifolia* (a true Cape Cineraria) and *C.* [*Agathæa*] *amelloides* do not appear to have succeeded; but between *C. cruenta* and *C. lanata* some handsome hybrids were raised. Since that time numerous experiments have been made and hybrids have been raised, etc." A summary follows.

Soon after this a number of definite seedlings or "sports" came into existence. Of some of these there are good records. I will mention four which are represented by good coloured plates. *C. waterhousiana* is said to have been a hybrid, the result of the seed of *C. tussilaginis*, fertilised by the pollen of *cruenta* (*Paxton's Mag. of Bot.* IV, 1838, p. 43, and *Ladies' Mag. l.c.*). In general appearance it rather resembled *tussilaginis* (one of L'Héritier's species which had died out, and was introduced again in 1832 by Webb. See *Bot. Mag.* t. 3215). This must have been a very fine plant. It had large *red* flowers, about two and a half inches across, with long narrow ray-florets something like *lanata*.

The next case I shall take is a plant which first flowered in a garden near Belfast, called var. *cyanophthalmus* in *Bot. Mag.* 1840, t. 3827. It had long white rays and a *blue* disc. Sir W. J. Hooker says of it: "Notwithstanding the very unusual colour of the flowers for one of the Compositæ, I have little hesitation in referring it to...the old *C. lanata* of our gardens. The foliage is the same, and the structure of the flowers; but the colour of the blossoms is very different, and in our variety of a most unusual character." He then recalls de Candolle's well-known remark that *yellow* in Compositæ may vary to red or white, but not to blue, and, on the other hand, that *blue* may vary to red or white, but never into yellow. He adds: "Not only in our plant is the lilac-coloured ray of the flower changed to white, and the deep lilac or blood-red purple of the ray [disc] changed to a very bright blue, but the stigmas, which are deep orange in the original stock, are also intensely blue, and the anthers are purple-black."

Another seedling of a very different type, famous in its day, was *webberiana*. It was figured in *Paxt. Mag. Bot.* IX, 1842, p. 125. The

flowers were of a deep blue, the rays being short and wide, compared to those of *waterhousiana*, for example. "It was raised from seed ripened promiscuously on a number of plants of various kinds blooming together, etc." In the *Gard. Chron.* 1842, it was advertised at 10*s.* 6*d.* a plant.

Another sport, pinkish and white, is figured in the *Botanist*, v. 1841, No. 215. "It came up accidentally, some years ago, from self-sown seeds, in one of the pots of the greenhouse, so that I cannot say anything certain about its parentage." The writer conjectures it to be a hybrid between *lanata* and *populifolia*, var. *leucanthus*.

If anyone will look at the plates to which I have referred, he may satisfy himself of the astonishing diversity of these forms. In *Gard. Mag.* 1839, p. 430, is an early record of the appearance of the new seedlings at shows. At the Caledonian Horticultural Show, the Cinerarias "were very brilliant, and partook of novelty." The names of the seedlings successful, including *waterhousiana*, are given. At the beginning of the 'forties the named kinds became very numerous, and were at first offered at high prices in the trade advertisements. Henderson and Ivery were the two chief English cultivators at that time.

During this period, 1830–1840, the progress was very rapid, and there can be no doubt that the florists' Cinerarias came into existence within some ten or twelve years. Such a plate as that in *Journ. d'hort. Gand*, 1846, shows the ordinary kinds much as we know them. From those plants up to the perfected plants of ten years ago the change was undoubtedly slow and gradual. The alterations have consisted chiefly in increase in size and symmetry of the flower, and in promotion of compactness of habit (see *e.g.*, Glenny, *Ann. of Hort.* 1850, p. 37, also *Gard. Chron.* 1879 (I), p. 532).

The next point is of some interest. As compared with other "improved" herbaceous plants, the Cineraria is a little peculiar in the fact that it is now generally raised from seed. This is done partly to ensure that the plants shall not be overgrown, and partly to avoid green fly, a pest to which these plants are specially liable. In consequence of this, the old "named" kinds, that is to say, kinds propagated by asexual methods, went out of fashion, though till lately they still had supporters. It was found that seeds of good strains could be fairly relied on—not, of course, to reproduce the form of their particular parents, but to give fine plants. For instance, Henderson, *Scot. Gard.* I, 1852, p. 22, says: "In raising seedlings you should select

three or four dwarf varieties, which number is quite sufficient to produce all the different colours." In *Gard. Chron.* 1887 (I), p. 549, are some interesting particulars of the methods used by Mr James, to whom the later improvement of the plant in England is largely due. The plants of each colour are grouped in blocks, and the bees are freely admitted to the houses. It is not found necessary to separate the plants further, and in saving seed all the colours are mixed together. In the case of the Cineraria, therefore, as in that of Calceolarias, Begonias, and other plants much grown from seed, it is desirable not only to create a fine variety of which the stock can at once be multiplied asexually, but also to raise a good strain of which the seedlings come fairly true. The latter process may undoubtedly often take time.

Even in recent times a "sport" has been recorded. In *Gard. Chron.* 1880 (I), p. 277, it is stated that Mr James "has succeeded in obtaining a new 'break' that promises to be the forerunner of another host of new flowers. The colours of the flower do not shade off into one another, as is usually the case, but are arranged in bold and well-defined belts. ...We understand that it flowered for the first time last season, and that it has reproduced itself from seed." A figure is given.

To these particulars might be added many more, relating to the origin of double varieties, variations in the foliage, and other matters. The foregoing notes of the history must, I think, be taken to show (1) that the modern Cinerarias arose as hybrids derived from several very distinct species; (2) that the hybrid seedlings were from the first highly variable; (3) that "sports" of an extreme kind appeared after hybridisation in the early years of the "improvement" of these plants; (4) that the subsequent perfection of the form, size and habit has proceeded by a slow process of selection. Mr Dyer's statement that the modern Cinerarias have been evolved from the wild *C. cruenta* "by the gradual accumulation of small variations" is therefore, in my judgment, misleading, for this statement neglects two chief factors in the evolution of the Cineraria, namely, hybridisation and subsequent "sporting."

I have ventured to deal with this case because it seems to be generally supposed by those not acquainted with the facts, that the origin of the modern florists' flowers has in general been very gradual. As a matter of fact it would, I believe, be more true to say that the new departures have in general been at first very rapid, subsequent improvement being commonly slow. "Sporting," usually after

hybridisation, has been the chief factor in the production of these new developments, just as in the case of the Cineraria. To speak of no more, I may refer to the new forms of Begonia, of Gladiolus, and of Erica now so familiar. With what special propriety the Cineraria was chosen by Mr Dyer to support his contention is not evident to me.

Whether any of these sports exhibit the phenomenon of organic stability I cannot now discuss.

THE ORIGIN OF THE CULTIVATED CINERARIA

[*Nature*, LII, 1895]

I MADE two objections to Mr Dyer's account of the history of the Cineraria; the careful reader will observe that his letter[1] meets neither. Mr Dyer informed us that the cultivated Cinerarias were produced "*by the gradual accumulation of small variations*," *i.e.* without the selection of definite sports. My object in adducing historical evidence of Cineraria sports was to prevent Mr Dyer's pronouncement from being repeated without further evidence. That purpose I think has been attained; for I notice that in now restating his account Mr Dyer does not refer to the point, though it was the object of his original exhibition of the Cineraria to the Royal Society. That the Cineraria was an excellent "illustration of the amount of Variation which could be brought about under artificial conditions in a limited time" I should be the last to dispute. As I showed in my first letter, there is evidence that the time was very short indeed.

Compared with this point, the second question—that of the hybrid origin of cultivated Cinerarias—is of subordinate interest. For the view that they were originally hybrids, resulting from crosses between *C. cruenta*, *C. lanata*, and other species, I have given the evidence, quoting the explicit statement of contemporaries and the almost universal opinion of practical gardeners, with references to the sources of information. Mr Dyer, however (with him Mr Rolfe), declares that they are descended from *C. cruenta* alone. Is this statement a mere inference from the want of likeness between particular cultivated Cinerarias and the wild species, or have Mr Dyer and Mr Rolfe evidence of a more substantial character? Of course these authorities may be right, and the rest who have written on the matter may be wrong; but I ask for proof of this, and the request can hardly be thought to be unreasonable.

Mr Dyer has referred to a remark I made at the meeting respecting the Camellia. At the risk of diverting attention from the real issues, I feel bound to speak of this, for I was then in the wrong. In justice the circumstances must be stated. Speaking of the Cineraria, Mr Dyer declared that though the flowers have changed so much, the foliage, which had not been an object of Selection, still resembled that of his wild plant. I replied that though this might be true of the

[1] [See *Nature*, LII, May 2, 1895, p. 3. ED.]

Cineraria, it led to no universal induction, for it is well known that the foliage of many plants selected solely for their flowers or for their fruits had varied greatly. As an illustration taken on the spur of the moment, I said that though the matter had not come within my own observation, there was, I believed, a passage in one of Darwin's books to the effect that the foliage of the several kinds of Camellia differed so much that they could be recognised by it alone. Upon Mr Dyer interjecting that this was not true, I immediately gave up the illustration as not coming within my own knowledge, and substituted that of the Apple, of which I myself know several kinds to have distinct and characteristic foliage. Such examples may be multiplied indefinitely. Now the passage in Darwin is as follows: "Verlot mentions a gardener who could distinguish 150 kinds of Camellia when not in flower" (*Animals and Plants*, ed. 1885, II, chap. XXII, p. 238); but Darwin takes the case as an illustration of the fact that structures "though appearing to an unpractised eye absolutely undistinguishable, yet really differ." My use of this case was therefore a wrong one, and as Mr Dyer has thought fit again to refer to the matter, I take the opportunity of withdrawing it once more.

THE ORIGIN OF THE CULTIVATED CINERARIA

[*Nature*, LII, 1895]

REFERRING to records of the history of cultivated Cineraria, I found (1) that considerable sports, or seedlings presenting notable and striking variations, arose in the early days of the "improvement" of the Cineraria; (2) that there is evidence that the improved varieties were of hybrid origin. I concluded, therefore, that Mr Dyer's statement that our Cinerarias have been derived from *C. cruenta* "by the gradual accumulation of small variations" was misleading in two respects. As we have now had the benefit of a fuller statement of Mr Dyer's case, I ask leave to explain why it is that I still hold to my original conclusion.

Meanwhile, however, Prof. Weldon[1], intervening, has offered an apparently sustained criticism of my evidence, which to those no better prepared may have a formidable look.

We will first examine some of Prof. Weldon's minor points. In preface let me say that I do not contend that *no* sports or named varieties have ever been believed to have arisen directly from *cruenta*, or from plants so-called (for, as Willdenow hinted[2], the name may have been misapplied to hybrids in the past as now); and, indeed, I gave Drummond's words that his *cruenta* "sported freely from seed."

Something was made also of the wise caution which Burbidge gives in his general "Introduction" (p. 118), putting the reader on his guard against specific assertions as to the origin of hybrids. I mention, therefore, that I have received from Mr Burbidge a latter warmly supporting the opinion given in the body of his book (p. 249) that the Cinerarias are of hybrid origin.

But now for what Prof. Weldon takes to be the real strength of his attack. He says that I omitted passages proving that according to contemporary opinion many of the named varieties cultivated between 1838 and 1842 "were not hybrids," but were "believed to be pure-bred *cruenta*." Upon what grounds this statement has been made, the reader shall now learn, not perhaps without astonishment.

[1] [See *Nature*, LII, May 16, 1895, p. 54. ED.]

[2] He says (*Enum. Pl. Berol.* 1809, p. 893) that Cinerarias are grown in gardens under the name *cruenta*, though really very different from it, having flowers almost like those of *lanata*. To these he gave the name *C. hybrida*. Moreover, from Bouché's experiment, we know that the seedlings of this *C. hybrida* were very variable.

The passage on which he chiefly relies is taken from Mrs Loudon's article (*Ladies' Mag. of Gard.* 1842, p. 111), to which I referred for the statement that in the writer's opinion the first important departure in the improvement of the Cineraria was made when Drummond hybridised *cruenta* with *lanata*. She goes on to say that, "since that time, numerous experiments have been made and hybrids raised" from several species. Next, that "some of the most beautiful Cinerarias now in our greenhouses have been raised by Messrs Henderson, Pine-apple Place, particularly *C. Hendersonii* and the King, both raised from seeds of *C. cruenta*." This is the passage I omitted. Prof. Weldon says that this "passage clearly shows that in the writer's [Mrs Loudon's] belief, the hybrids produced by Drummond and others had not given rise to two at least of the named varieties of her time," and that she believed the King and *Hendersonii* to be descended from *cruenta* alone. This Prof. Weldon tells us is certain.

Now, were we even bounded by the limit Prof. Weldon has set to his own researches on this question, we might hesitate to assume that whenever it is not expressly declared that a plant is a hybrid, we may be sure that the author thought it was pure-bred. As it happens, however, I can meet the charge with a weapon sturdier than the fine point of "dialectic." The answer is quite simple and curiously complete.

I shall now prove that both the King and *Hendersonii* were well known as hybrids both to Mrs Loudon and to others. Let me point out:

(1) That the words say that the King and *C. Hendersonii* were raised from *seeds* of *cruenta*: as to the *male* parent, nothing is there said.

(2) That even if the evidence ended here, a discriminating reader might have suspected (what I shall presently prove) that Mrs Loudon's *particular* statement about the King, *Hendersonii*, etc., is merely meant as an expansion of her previous *general* statement that since Drummond made his beginning numerous hybrids had been raised.

(3) That, were the matter doubtful, other passages in Mrs Loudon's works prove this to be her meaning. For in *Ladies' Comp. to Flower-Gard.* 1849 (*s.v.* Cineraria), she states, "the finest hybrids are *C. Waterhousiana*, *C. Hendersonii*, and the kind called the King." Again, in *Ladies' Flower-Gard., Greenho. Plts.* 1848, p. 178, speaking of the woolly leaves, etc., of *lanata*, she says, "these peculiarities are found in all the numerous hybrids that have been raised from it. Perhaps

the most ornamental of these is the hybrid called the King[1]." Of this, therefore, I presume Mrs Loudon believed *lanata* to be the father, *cruenta* the mother.

(4) Lastly, that in order to have learnt that the King and *Hendersonii* were "between 1838 and 1842" considered to be hybrids, Prof. Weldon need not have gone far. He tells us he has read the articles on *C. Webberiana* (*Paxt. Mag.* 1842, p. 125) and on *C. Waterhousiana* (*ibid.* 1838, p. 219), to which I gave references. Will it then be believed that in the first of these very articles *the King is referred to by name as a notable hybrid*; and that in the second article, "*C. cruenta*, var. *Hendersonia*" is with others named as *one of "the hybrids raised and grown by Messrs Henderson, Pine-apple Place"*?

I do not know if it is wished that I should further refute Prof. Weldon's charge of "want of care in consulting and quoting the authorities." I am not unprepared to do so. I shall be glad to explain why Mrs Loudon was probably right in substituting the name *tussilaginis* for *tussilagofolia*; to show why *Webberiana*, price 10*s.* 6*d.* (*Gard. Chron.* 1842, p. 665), may be called a striking advance on its contemporaries, price 2*s.* 6*d.* (*Gard. Chron.* 1842, p. 633), together with many other matters not yet treated of in this discussion.

My first objection to Mr Dyer's statement was taken on the ground that there is historical evidence that sports, or seedlings presenting notable variations, occurred in the early days of the improvement of the Cineraria. To this, after reading his letters with great care, I do not find any specific answer. He tells us that the history as he gave it would be "in accord with general horticultural experience." It obeyed then a rule to the proof of which exceptions are indeed not lacking. He says, further, that to improve a plant the only safe way is by "selecting the minutest trace of change in the required direction," and "by patiently and continuously repeating the operation." Now this would be all very well if we knew nothing about the origin of the Cineraria; but against the evidence that seedlings presenting striking variations did as a fact arise, and against the historical evidence that Cinerarias, much as we know them, did as a fact come into existence

[1] So famous a hybrid was the King, that I regret that I did not mention it in my first letter. I did not do so, as I found no coloured plate of it. Mr John Fraser, of South Woodford, kindly informs me that he remembers it as the best of the woody sorts formerly grown. Its flowers were about the size of a penny, rays white tipped with purple, leaves downy and of a silvery hue on the underside. Its seedlings were unreliable.

within some twelve years, such *à priori* expectation is worth nothing at all.

To my second objection, that there is evidence that the chief start in the improvement of Cinerarias came as the result of hybridisation, Mr Dyer has given more attention. He proposes to meet it by rejecting the whole of the historical evidence as unsound, and preferring the conjecture to which he says an inspection of the modern plants has led him. The historical evidence is to go because we are told certain horticulturists are ignorant men. I premise that this is not a principle which Darwin, whom Mr Dyer would claim as his master, would have endorsed.

But before judging, let us try to consider what was the objective evidence on which the gardeners made up their minds that the new Cinerarias were hybrids. I may illustrate this by reference to a seedling now growing in the Cambridge Botanic Garden, to which Mr Lynch, the curator, kindly called my attention. The case is of special interest in view of Mr Hemsley's objection that it requires skill and care to raise a hybrid in the Compositæ. It was with regret I learnt that this careful writer was not with me in this matter.

This seedling was raised from a seed of our plant of *lanata*, which was received from and is exactly similar to those at Kew[1]. In habit and size our seedling is not at all like *lanata*, but might be taken for a poor specimen of the common Cinerarias. In several characters it is intermediate between *lanata* and the latter. The stem is rather woody, less so than in *lanata*, but it is thick like those of garden kinds: petioles like *lanata* in having no auricles: leaves, nevertheless, large like those of garden kinds, the backs very woolly, but largely purplish, as in many cultivated sorts. Now this plant must be either (1) a sport from *lanata* in the direction of the garden forms, or (2) an accidental hybrid between *lanata* and one of the cultivated kinds growing in the same house with it (we have no others). The latter seems more likely —an opinion in which Mr Lynch fully concurs.

Similarly Bouché (*Wittm. Monatss.* XXII, p. 298, orig. not seen, quoted from Focke, *Pfl. Mischlinge*, 1881, p. 201) says that a hybrid between *C. Webbii* (Schlz. Bipont.) and *cruenta* arose in the Berlin Botanic Garden as the spontaneous product of these species growing side by side.

[1] There labelled *Héritieri* (of DC. = *lanata*, L'Hér.). I note that though otherwise agreeing exactly with the *lanata* described by L'Hér., de Candolle and Webb, the inflorescence of these plants differs, being a loose corymb of some twenty heads, instead of the single flowered peduncle (*rami semper monocephali*, Webb) of the old authors. Whether this variation is known in wild plants, I cannot tell.

It was, I think, on evidence like this that the parentage of the older hybrids was conjectured; but that Drummond and Henderson certainly—and possibly others—did make definite efforts to hybridise, cannot on the evidence be doubted. That these efforts went no further than the brushing of pollen of some species upon the flowers of others, I fully believe, and that on such evidence the *precise* parentage cannot be assigned is obvious. Nevertheless distinct seedlings resulted. In a few years, as the writer in *Paxt. Mag.* 1842, p. 125, says (in an article urging to fresh efforts in crossing), this hybridisation "was the means of creating quite a novel and superior race." There were the new plants: how had they arisen? Those who doubt that these new kinds were hybrids must choose the other horn of the dilemma, and accept them as sports pure and simple.

That the historical records may contain errors, I am fully aware; but if they cannot be accepted in detail, should they be altogether rejected? We might perhaps reserve a doubt whether the King came precisely from pure *cruenta* fertilised by *lanata*; whether *cruenta* var. *latea* was a hybrid between *cruenta* and *populifolia* (as de Candolle surmises); whether *Waterhousiana* was the offspring of true *cruenta* and true *tussilaginis*; whether Mrs Loudon's statement that the species used were *cruenta*, *lanata*, *aurita*, *tussilaginis*, and *populifolia*, or Moore's belief that *cruenta* and *tussilaginis*, with perhaps *Héritieri* (= *lanata*), *maderensis* (= *aurita*), and *populifolia* (*Cross and Self-Fert.* p. 335, *note*), or Otto's similar declaration (Regel's *Gartenflora*, 1857, p. 66), or that of the *Journ. d'hort. Gand*, 1846, already given, should each be taken without hesitation as full and complete statements of the whole truth, but that they contain a substance of truth is hardly in question.

Against this Mr Dyer offers nothing but an opinion derived from an inspection of certain modern plants. He who has confidence in the results of this method must suppose our knowledge of the laws of inheritance to be much more complete than I believe it to be. It is not the method Darwin used. Take a well-ascertained case. Who would know from inspection of the Himalaya rabbit that it came directly from the Silver-greys or Chinchillas? (See *Animals and Plts.* I, p. 113.) It is unlike them, is of sudden origin, and yet breeds true[1].

[1] To Mr James, of Farnham Royal, a celebrated grower, and to his foreman, I am indebted for several interesting points, and especially for the following: Formerly blue self-coloured Cinerarias were scarce in his strain, but some years ago he introduced some plants of a French strain. After this, and presumably as a result of the

To suppose that in cross-bred offspring given characteristics of the parents must be found, is to assume the precise question which in a discussion of organic stability is at issue. Let it be remembered that on the hypothesis of hybrid origin for our Cinerarias it is supposed that they result from several species and varieties, crossed not once only, but many times, in wholly irregular ways. Can it be seriously expected that any special resemblance to a given ancestor should be still traceable[1]?

My position then is this. We heard Mr Dyer's statement; turning to the literature I found an entirely different account, borne out by copious and on the whole fairly attested evidence, pointing irresistibly to the conclusion that the Cinerarias are species which hybridise freely, and that our modern forms have arisen through such hybrid unions.

Mr Dyer has well said that "if you take any statement that Mr Darwin has put forward, you may feel assured that behind it is a formidable body of carefully considered evidence not likely to be upset." By the courtesy of an opponent I have been directed to a passage in *Cross and Self-Fertilisation*, 1876, p. 335, where (before describing experiments showing considerable self-sterility in the garden Cineraria) Darwin gives this definition of his material, "*Senecio cruentus* (*greenhouse varieties, commonly called Cinerarias, probably derived from several fruticose or herbaceous species much intercrossed*)." It seems, therefore, that in this matter also Mr Darwin has, to use Mr Dyer's words, "squeezed out" of the evidence "all that it would profitably yield."

Here I would fain leave the subject. But perhaps it may be suggested that though Darwin's Cinerarias were probably hybrids, our Cinerarias may not be their descendants. Such a suggestion involves the supposition that in some hidden place there was a thin red line of pure *cruenta* waiting for the moment when it should oust the hybrids. If this be seriously suggested, I shall ask where such a strain was kept, and what steps were taken to preserve its purity. In view of the evidence that chance blendings occur freely, to keep a

cross between his own and the French kinds, there appeared a strain of blue selfs. These, though shy seeders themselves, transmit their peculiarity so strongly that they have to be kept in a house apart, for fear that their character should assert itself to the exclusion of everything else.

[1] In order to meet Mr Dyer on his own ground, I have assumed, what I cannot admit, that in none of the various modern strains traces of the different parent-species appear.

pure strain would require some care. Until this has been proved, we shall not, I think, be wrong in supposing that each grower worked on the material his predecessors had created, and that our Cinerarias are the lineal descendants of the hybrids raised in the first half of this century.

In the course of this discussion, Mr Dyer has treated me to some hard words, which I do not particularly resent. Whether I have deserved them is not, perhaps, for me to judge. But I will ask Mr Dyer to point out when, on being asked for the facts upon which I have based a view, I have replied that that was a "matter for future collection." The facts I have been able to collect may be few, but by a study of the writings of my antagonists, I have not been able to add materially to their number[1].

[1] It has been impossible for me to incorporate in this letter all the mass of information which has been most generously sent me by correspondents since this controversy began. It is suggested that I should point out that Mr Dyer's use of the word "feral" to mean "wild" is not usual. A correspondent tells me that it was probably first used in the special sense of "run wild" by Hamilton Smith, *Nat. Libr. Mammalia*, 1839, IX, p. 92. It has since been so used by many authors, especially Darwin, *An. and Plts.* I, p. 117, etc.

NOTES ON HYBRID CINERARIAS PRODUCED BY MR LYNCH AND MISS PERTZ

[*Proceedings of the Cambridge Philosophical Society*, 1897]

IT is stated by many writers that the garden Cineraria arose as the hybrid offspring of several species of *Senecio* from the Canary Islands. This statement has been questioned by Mr Thiselton Dyer on various grounds. The author exhibited hybrids raised from *S. cruentus*, *S. multiflorus* and *S. Heritieri* (= *lanatus*) raised in the Cambridge Botanic Gardens by Mr Lynch and Miss Pertz which illustrated the great variability which appears in the offspring of the various crosses. In particular, specimens of *Heritieri* ♀ × *cruentus* ♂ and of the reciprocal cross were produced, showing excessive variability and proving how greatly the peculiar characters of *Heritieri* may be obscured in the offspring, even of the first cross. Five specimens of *multiflorus* ♀ × *Heritieri* ♂ were exhibited, each of which was quite distinct from the rest. Experiments had entirely confirmed Darwin's observation that Cinerarias are self-sterile in a high degree. They hybridise on the contrary with great readiness. An accidental hybrid between *Heritieri* ♀ × garden Cineraria ♂ and the reciprocal were also shown, the two plants being quite unlike each other, the former being an upright plant of a rather woody habit, resembling poor specimens of the garden Cineraria, while the reciprocal (illustrated by two specimens of independent origin) was a struggling plant with large pale flowers having almost a procumbent habit, differing considerably from both its parents. One seedling *multiflorus* ♀ × garden Cineraria ♂ had been produced which was almost entirely female, a few anthers only appearing in later inflorescences. These experiments were to be continued, but so far as they had gone they were entirely consistent with the view that the Cineraria was a hybrid between several species, *cruentus*, *Heritieri* and probably *multiflorus* being among them. The two first are named by most authorities as probable parents.

It was proposed to publish details of the experiments when those of the next year should be completed.

ON THE COLOUR-VARIATIONS OF A BEETLE OF THE FAMILY CHRYSOMELIDÆ, STATISTICALLY EXAMINED

[*Proceedings of the Zoological Society*, 1895]

(With Plate VI)

At a meeting of the Society on May 1, 1894, I exhibited living specimens of *Gonioctena variabilis* in illustration of the remarkable range of colour-variation in the species. Since then I have had opportunities for a fuller investigation of the matter, and the following paper is an account of the results obtained.

G. variabilis[1] is a small beetle, about $\frac{1}{4}$ inch long, belonging to the family Chrysomelidæ. It lives on *Spartium retama*, a plant allied to the common broom, very generally distributed in hilly places in the south of Spain, though absent, I believe, from the limestone districts. This plant grows as a bush varying in height from one to about seven feet according to the situation, humidity, and exposure. The stunted form is dense and compact, having stout branches spreading out more or less horizontally, giving off erect leaf-bearing stems set closely together. The tall form is slender and graceful, and its leaf-bearing stems are generally pendulous and wavy. In their extreme forms these two conditions of the plant differ considerably from each other, but all intermediate conditions are found.

In colour the stems of this *Spartium* are of a dull greenish grey. The surface is marked with irregular longitudinal ribbings, which give it an appearance of faint striping. It is upon the stems of this plant that the beetles live, infesting both forms indifferently. When at rest they are commonly seen sitting with their heads in the axils of the twigs, their bodies being closely pressed against the surface. Several other species of *Spartium* grow in the south of Spain, but I did not find *G. variabilis* on any of them. Nevertheless, living specimens brought home to England ate the shoots of *S. juncifolium*, with which they were provided from the Cambridge Botanic Garden.

It was at Granada, on March 28, 1894, that I first saw *G. variabilis* and was at once struck by the great variety of appearance presented by different individuals. In a few minutes I came upon most of the chief kinds, including what will be described as the red form with black spots, the greenish-grey form with black stripes, a totally black

[1] The genus *Gonioctena* is *Phytodecta* of the Munich Catalogue. The species *G. variabilis* is the *Phytodecta ægrota* of Fabr. and Suffr.

form, etc. As may be seen from the figures (Pl. VI) these different varieties are strikingly unlike in general appearance, and not having previously heard of this beetle I at first doubted whether all were one species. Then, finding specimens of dissimilar colours coupled together, I concluded that they did all belong to the same species, and as all intermediate forms were afterwards found, there can be no doubt on this point. Subsequently Dr D. Sharp, to whom I am indebted for much help in examining these specimens, gave me the name of the beetle and told me that it was known to undergo great variation in colour[1]. I may add further that no difference could be seen in examination of the ædeagus of the several forms.

It appeared that the case was worth further investigation with the object of determining with what frequency the various colours occur, and to what extent specimens collected at random could be grouped round special type-varieties to the exclusion of intermediate forms, thus manifesting the phenomenon known as organic stability in respect of those varieties. As so many specimens were found *in cop.* it seemed further that by recording the colours of specimens so coupled it might be possible to get an indication whether there existed any operative sexual selection as to colour.

The next few days were spent in gathering a sufficient sample, and I then returned to Gibraltar to follow other work. Very soon, however, I found that the colours had so faded that the collection already made was useless for my purpose. In fact, in dried specimens the red and the green both usually fade to an indifferent brown. I therefore went back to Granada and gathered a fresh sample of about 1500. These I put into a large wooden box and brought alive to England. In the following year (1895) I returned to Granada and collected, on March 24–28, about 2500 more, recording all the colours at the time.

It at once appeared that the colour is to a great extent dependent upon sex, the males being generally of the red form with spots like Fig. 1, while the females are generally of the greenish form with stripes like Fig. 23, though every colour is sometimes found in each set. For this reason, before sorting the specimens for the purpose of determining the frequency of each colour, it is necessary first to sort them in respect of sex. This can be done without much difficulty. Besides a slight difference in shape and in sculpture (which gives to the elytra of the female a duller lustre) there is a well-marked de-

[1] Several varieties have been briefly described by Weise (*Deut. ent. Zeitschr.* 1891, p. 160), but I infer that the colours were given from dried specimens.

pression or pit in the last uncovered abdominal plate of the male, while in the female there is no such depression.

In attempting to arrange or group the specimens according to colour, confusion is caused by the fact that variation occurs in several distinct features. Of these the three most noticeable are:

(1) The ground-colour of the elytra.
(2) The distribution of black pigment on the elytra.
(3) The colour of the legs and underside of the body.

Since the variations of the first two points are largely independent, it is not possible to exhibit the relationships and frequencies of all the variations by arranging the specimens in *one* series. The whole number, males and females, can, however, be seen to consist of two chief kinds—the one distinguished by having four *black spots* on the elytra (Figs. 1–6, etc.) and a dark, generally black, underside to the body, while the other has an appearance of *black striping* on the elytra (Figs. 20–23) associated with a light testaceous underside to the body. Those with undersides that cannot at once be referred to either the dark or to the light division are rare; in the Tables given they are included under the heading "unconformable." In those with light undersides the legs are of a similar testaceous colour. If the underside is black, the femora are generally black too; but frequently the coxæ and tarsi, and less often the tibiæ, are of a lighter colour.

Examined closely the distinction between the distribution of the spots and the stripes is seen to be as follows: The striping consists of pigment deposited in certain positions that can be defined pretty accurately by reference to the punctulations. These are somewhat more regularly disposed in the female than in the male, but by standing back to the light and looking at the specimen from behind it can be seen that the following arrangement is fairly constant. Following a line across the middle of an elytron there is next to the suture a double row of punctulations. External to this is an interval. Then come the 2nd–8th double rows of punctulations separated by intervals. Outside the eighth interval is a 9th row of punctulations, which is irregularly treble.

It is in the four intervals between the 2nd and 3rd, 4th and 5th, 6th and 7th, 8th and 9th double rows that the four chief tracheæ of the elytron run; but the four principal stripes of pigment are placed in the *other* intervals, viz. between the 1st and 2nd, 3rd and

4th, 5th and 6th, 7th and 8th double rows of punctulations. There are not rarely a few dots of pigment in the other intervals, and, in the case of heavily striped specimens, these sometimes unite to form secondary stripes.

The definite "spots," however, that are associated with the black undersides (as in Fig. 1, etc.) consist of patches of pigment usually placed so as to *cross* respectively the one the 2nd, 3rd, and 4th, the other the 7th and 8th double rows of punctulations. The extent of these spots varies greatly and in its condition of least development the central of the two spots coincides very nearly with the 3rd double row of punctulations, and the lateral spot similarly is very nearly on the 7th double row.

All these arrangements are liable to irregularity, but in the main they are as described, and essentially in the spotted form pigment *crosses* certain of the double rows of punctulations, while in the striped form it is almost entirely in the *intervals* between them.

The association of the black spots on the elytra with dark underside is exceedingly close, and it scarcely ever happens that a specimen which has black pigment in the position of the spots (Fig. 1) has a light underside. This principle is obeyed whatever the ground-colour of the elytra may be. Figs. 25 and 26, 28–30 are given as illustrations of specimens in which the rule is not followed, the undersides not being black though there is black pigment on the elytra in the situation of the spots.

This division into spotted forms with dark undersides and striped forms with light undersides is the most conspicuous feature in the variation of the insect. In great measure the distinction is sexual, most of the males belonging to the spotted division and most of the females to the striped. Curiously the number of each sex which belongs to the opposite group is about the same, for on sorting it appears that

Of *males*	about	80	per cent. are of the	spotted	class.
,,	,,	18	,, ,,	striped	,,
Of *females*	,,	25	,, ,,	spotted	,,
,,	,,	71	,, ,,	striped	,,

This reckoning is made without reference to ground-colour, and specimens that have striping as well as spots are of course included in the spotted class, to which they belong also by reason of their dark undersides.

Of the spotted form the great majority (73 per cent. of all males and 19·6 per cent. of all females) have red as the ground-colour of the elytra. Of the striped form, on the other hand, the majority (19 per cent. of all males and 65·7 per cent. of all females) have greenish grey as the ground-colour. In fact the great majority of males agree pretty closely with Fig. 1, while the great majority of females resemble Fig. 23; but of the males the *next commonest* form is that shown in Fig. 23, and of females the second commonest is that of Fig. 1. It thus appears that the form which may be called normal for the female is the commonest variety in the male, and the converse is true though to a less degree.

The thorax of the striped forms usually has black pigment as two black spots (see Figs. 19–24), while in the spotted forms the thorax is generally black with some lighter colour at the periphery and not rarely in the middle line.

Considering the *ground-colour* of the elytra there are thus two chief kinds, red and greenish grey. The majority can at once be referred to one or other of these two. Nevertheless there are intermediate colours forming an unbroken series or transition from the one to the other. Such a series is represented in Figs. 1–6. Starting from the bright red kind (Fig. 1) and passing through a duller red (Fig. 2) a neutral buff (Fig. 3) is reached. This buff is almost exactly intermediate between the red group and the greenish grey. The next stages in the transition are yellow (Fig. 4), yellowish green, and greenish grey (Fig. 6).

Taking *spotted* males alone the bright reds are by far the commonest, the duller reds are the next commonest, the buff are very rare, while yellows and greenish together make up a fair group. As to the relative frequency of these yellows and greens, the data are unreliable. The total number belonging to these classes was small, and it is not possible to sort them among themselves with any strictness. I am satisfied that the yellows are more common than the buffs, and the *spotted* greenish greys are probably less common than the yellows; but of this I am not sure. In the Table given at the end I have united them.

Of *striped* males almost all are greenish grey. Reds and yellows occur, but are exceedingly rare. The whole number of striped specimens with a ground-colour other than greenish grey is so small that it is not possible to judge the frequency of the respective colours. I attempted for some time to distinguish different shades of the greens according to the degree of yellow. But while certain of the striped

kinds are obviously yellow and others are obviously yellowish green, it was not found possible to sort consistently the yellowish greens from the greens with less yellow, so this attempt was abandoned.

With a view to determining the nature of the colouring matters, an examination of some specimens was very kindly made by Dr H. C. Sorby. The material sent to him consisted of a few of the reds and a few of the greenish form separately killed and preserved in alcohol. Dr Sorby informs me that the red pigment is slowly dissolved out by alcohol and carbon bisulphide, and when in solution in the latter is of exactly the same character as the similar pigment of the common lady-bird (*C. bipunctata*). After long action to dissolve out all the pigment of the elytra, the red form is left of a yellow colour, exactly like that which is assumed also by the greenish kind. Dr Sorby therefore conjectures that the reds differ from the others mainly on account of the development of the red pigment which is not found in the others. It is therefore possible that the ground-colours intermediate between the red and the greenish may be due in some measure to a difference in the amount of red pigment; but it seems likely that in the case of the yellow, which is a distinct colour, there must be an alteration in the nature of the pigment.

Specimens are occasionally found having the elytron of one side red and that of the other side yellow (Fig. 31). Not very rarely also there are more or less distinct patches of yellowish colour on the red ground, as in Fig. 32, where they happen to be nearly symmetrical. These specimens are included in the Tables under the head of "unconformable."

In addition to the varieties already mentioned, there is also a series of melanic forms. We have seen that the black pigment of the elytra may either take the form of stripes or of spots. From the latter group (Fig. 1) a noticeable series of variations leads to a form totally black above and below. Such a series is illustrated by the Figs. 7–12 and 15–18. The first step in the progressive pigmentation consists in the appearance of black in the positions of the stripes, which is gradually extended. These specimens are thus both spotted and striped. The parts last invaded are the apices, the shoulders, and the borders of the elytra[1]. The spread of the black is perhaps never

[1] Curiously enough, the two specimens figured by Olivier, *Hist. Nat. des Insectes*, Pl. VIII, fig. 127, *c* and *d*, are both of these very melanic forms. The locality is not given, and perhaps the frequency of the varieties may differ with locality.

quite symmetrical on the two sides and is not rarely noticeably asymmetrical to the degree shown in the figures.

The series of progressive pigmentation is closely parallel to that seen in *Coccinella bipunctata*, the common lady-bird.

Though the invasion of the black pigment proceeds along tolerably regular lines, darkening the parts of the elytra in a fairly constant order, yet as regards quantity of pigment variation towards the black form proceeds continuously, the states becoming successively rarer as the full black is approached. From the fact that the progress is so even it is not easy to give numerical expression to this; but on sorting the specimens which have more black than Fig. 1, it is found that while there are many which approximate to Figs. 7 and 8, there are fewer which resemble Figs. 9 and 10; those with only a few specks of red, like Fig. 11, are still rarer, while the totally black state is rarer than any of the others.

The darkening of the head and thorax proceeds more or less evenly with those of the elytra, but the correlation is not strict.

These melanic forms are, as has been said, an offshoot of the spotted kind and not of the striped. They have red as the ground-colour almost without exception. Fig. 26 represents the darkest specimen I have seen with greenish ground-colour.

A few specimens are found without any black markings on the elytra at all. These have the undersides testaceous. In such specimens the thorax has generally very little pigment and is occasionally entirely without any.

There is some suggestion that the frequency of the different variations may be in part dependent on locality. The great mass of my specimens were collected on the hills that extend behind the town of Granada, separating the two valleys of the Genil and the Darro. In the first year I made a separate collection also from the *Spartium* growing near the bottom of the Darro valley. I noticed at once that the proportion of the striped forms with greyish-green ground-colour was much larger than it had been in the case of the hill-locality. Unfortunately I was not at that time expert in sorting the sexes, and this Darro sample was eventually mixed with the rest that I brought, living, to England. The colours were recorded, but without reference to sex.

The second year, however, I made another attempt to get statistics of the Darro population, and give the result in Table II. The total numbers are unfortunately small, as the available area on which the

Spartium grows is not extensive; but the quantity is sufficient to show that the proportions are markedly different from those of the hill-sides, for while on the hill-sides 19 per cent. of males are of the striped greenish grey, in the Darro valley about 37·7 per cent. are of that colour. I am disposed to think this difference in proportion is a perfectly genuine phenomenon and not merely an accident of collection, but I can suggest no cause for it. The difference in altitude is very slight, averaging, perhaps, 300 feet. No doubt the Darro bushes are rather larger and better watered, but many of the bushes on the hills are of the same character and I did not find a high proportion of greens on them. The Darro valley is no doubt less exposed and rather hotter than the hill-sides, but it would not be easy to point to a specific difference.

A peasant employed as a "Guardia Municipal," with whom I made acquaintance, collected for me a considerable sample of some hundreds from Pinos, higher up the Genil valley. The proportions agreed fairly with my Granada sample; but as I knew nothing of the way in which they had been collected, the numbers are not worth giving.

On March 20, 1895, during an interval between trains at Castillejo[1], a place not far from Toledo, in a hasty sweeping I got 75 specimens, only one being a female. Of these none are of the striped greenish-grey form. The number is of course too small to justify a conclusion; but the result is remarkable, for according to the Granada experience there should have been about 14 such specimens. It is possible that in this more northern locality the proportions may be different. The scarcity of females is also to be noted and may perhaps be due to comparative backwardness of the season.

It seems that at Granada at all events the beetles are to be found for a considerable part of the year, for Mr Nicholson has kindly sent me a small gathering made in the month of June.

In the Table the frequency with which specimens of each colour were taken *in cop.* is recorded. In each case special care was taken to see that the pair were actually coupled, and none were counted for this purpose unless they remained attached when removed from the bush. It will be seen that the numbers agree very fairly well with those that they should be if the coupling occurred by simple chance, for the number of each colour found coupled bears about the same

[1] As travellers from Toledo for the south generally have to wait some hours at Castillejo, it is not unlikely that some entomologist may find an opportunity of looking into this matter. The *Spartium* grows in quantity near the station.

proportion to the whole number found coupled that would be expected according to the frequency of that colour.

It is clear that we have here an example of a species whose members exhibit variation in several different respects, and that the variations occur in such a way that the individuals must be conceived as grouped round several subtypical forms. There is thus not one normal for the species but several. Next, though all are living in the same locality under the same conditions, and though they breed freely together, these various forms are commoner than the intermediates between them[1]. Upon the significance of such a case I have sufficiently commented elsewhere[2].

One point may be of interest to students of the adaptation of the colours of animals to their surroundings, namely the fact that while the red-spotted forms are strikingly conspicuous objects the striped greenish-grey forms resemble so nearly the colour of the twigs of the *Spartium* that it is impossible not to remark the likeness. If they were the only form known, the case might well be used as an illustration of a protective coloration. The red-spotted forms present some superficial likeness to the common lady-bird (*C. bipunctata*), a creature which exudes an acrid juice, and whose colour has naturally been classed among "warning colours." The *Gonioctena* does not, so far as I know, possess any such irritant properties, but I have no information as to its enemies. As *Coccinella bipunctata* is not very common on the *Spartium*, probably no one will suggest that we have here an example of protective mimicry. I may mention, however, that *Coccinella septempunctata*, the larger scarlet species, occurs in vast quantities mixed with *Gonioctena*. Whether anyone would consider the resemblance to this species sufficiently close to constitute mimicry, I cannot say.

Speaking of the excessive variability of the colour of *C. decempunctata* and of the no less striking constancy of *C. septempunctata*, which lives with it, I remarked[3] that to ask us to believe that the colour of the one is constant because it matters to the animal, and that the other is variable because it does not matter, is to ask us to abrogate reason. Mr A. R. Wallace, in a recent article[4], takes exception to this comment, saying that he, for his part, is of this very

[1] As was pointed out, this is not true of the *black* variety.
[2] *Materials for the Study of Variation*, 1894, pp. 48, 72, etc.
[3] *L.c.* p. 572.
[4] *Fortnightly Review*, March 1895, p. 436.

TABLE I.—*Granada*, 1894 *and* 1895.

Collected on the hills between Darro and Genil.

	Swept	Taken *in cop.*	Totals	Per-centage
MALES				
Undersides dark				
Spotted: ground-colour bright red	1657	139	2186	73·7
„ „ duller red	390			
Spotted and striped, tending towards black } ground-colour red	177	9	186	
Spotted: ground-colour reddish buff	39	—	39	
„ „ neutral buff	25	—	25	
„ „ yellow to greenish grey	100	12	112	
Black all over	7	1	8	
Striped only: ground-colour greenish grey	3	—	3	
No stripes or spots: ground-colour red	1	—	1	
Unconformable	35	3	38	
			2598	81
Undersides light				
Striped: ground-colour greenish grey	596	24	620	19
„ „ red	5	—	5	
„ „ yellow	1	—	1	
Spotted and striped: ground-colour greenish grey	2	—	2	
No stripes or spots: ground-colour plain red	2	—	2	
Unconformable	2	—	2	
			632	19
Total captured		188	3230	
FEMALES				
Undersides dark				
Spotted: ground-colour red	102	27	129	19·6
Spotted and striped, tending towards black } ground-colour red	42	9	51	
Spotted: ground-colour buff	5	—	5	
„ „ yellow to greenish grey	34	13	47	
Black all over	9	3	12	
Unconformable	5	3	8	
			252	27·5
Undersides light				
Striped: ground-colour greenish grey	497	116	613	65·7
„ „ yellow	26	14	40	
No black: „ plain red	1	1	2	
Unconformable	8	2	10	
			665	72·5
Total captured		188	917	

TABLE II.—*Darro Valley*, 1895.

	Swept	Percentage
MALES		
Undersides dark		
Spotted: ground-colour red	341	58·3
„ „ duller red	41	
Spotted and striped, tending towards black: ground-colour duller red	37	
Spotted: ground-colour buff	5	
„ „ yellow to greenish grey	17	
Black all over	3	
Unconformable	3	
	447	62·3
Undersides light		
Striped: ground-colour greenish grey	270	
No black: „ red	1	
	271	37·7
Total captured	718	
FEMALES		
Undersides dark		
Spotted: ground-colour red	9	
Spotted and striped: ground-colour red	7	
Spotted: ground-colour buff	5	
„ „ yellow to greenish grey	6	
Black all over	1	
	28	14·4
Undersides light		
Striped: ground-colour greenish grey	164	
„ „ yellow	3	
	167	85·6
Total captured	195	

opinion. On the question *how* it is that the colour of *C. septempunctata* is so important, and the colour of *C. decempunctata* unimportant to the animal, I do not find Mr Wallace offering evidence, and I am not aware that he has even hazarded a guess. Meanwhile I wish to repeat in regard to *G. variabilis* what I said before in the case of *C. decempunctata*, that its several varieties exhibit that kind of definiteness and constancy to their respective types that we associate with the idea of species; but for supposing that this constancy is in any way dependent on adaptation to environment, we have no warrant.

Explanation of Plate VI[1]

These figures have been drawn by Mr Edwin Wilson from the living specimens. The colours were very carefully copied, but it was not thought necessary to reproduce the sizes and shapes of the individuals. The figures are about twice the natural size.

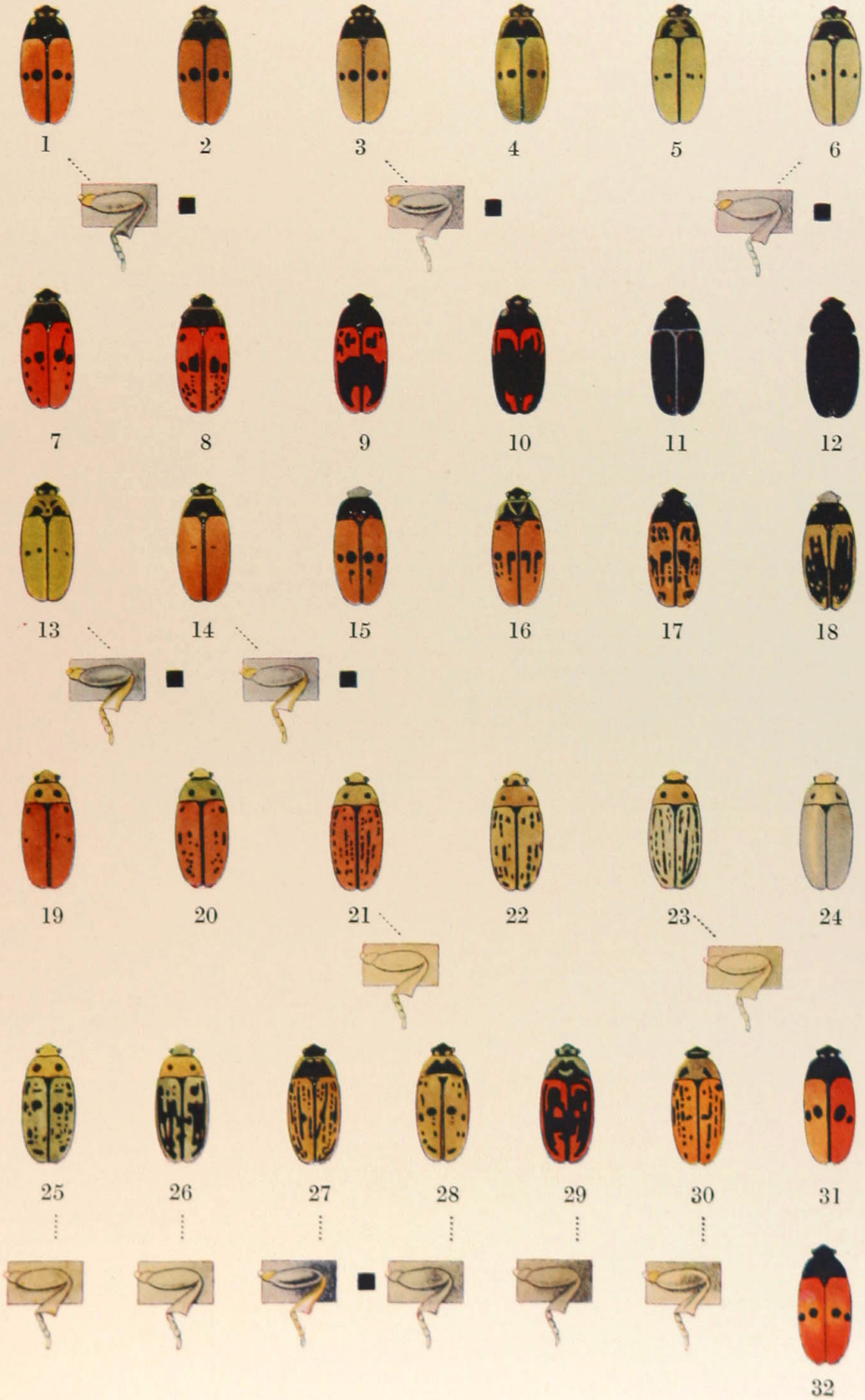
With the exception of Figs. 18, 22, and 27, which represent females, all were taken from males.

Figs. 1–6. Series illustrating the change of ground-colour from red to greenish grey.
Figs. 1, 7–12 are a series illustrating the progressive invasion of black pigment.
Figs. 13–18. Various forms illustrating diminution and increase in amount of black pigment.
Figs. 19–24. Forms with light undersides.
Figs. 25–30. Unconformable cases.
Figs. 25, 26, 28, 29, and 30 show specimens having light undersides, though they have transverse black markings in the position of the spots.
Figs. 27 and 28 are peculiar in the fact that, though melanic forms, the ground-colour is yellowish buff instead of red.
Fig. 30. Underside of intermediate colour, associated with a slight indication of transverse black marking.
Fig. 31. Specimen having right elytron red and the left yellow.
Fig. 32. Specimen having patches of yellow on red elytra.

The undersides were black in the case of Figs. 1–18, 27, 31, and 32; light in the case of Figs. 19–26; of intermediate colour in the case of Figs. 28–30.

A leg is drawn in some cases, and the small square beside it represents the colour of the underside without shading. The elytra are all coloured as if they had no high light on them, in order to give the colour more correctly, but actually they reflect a bright light.

[1] [The original plate was made by colour lithography. From it the present one has been reproduced by the colour block process. Ed.]



Variations of *Gonioctena variabilis*

WEBBED FEET IN ANTWERP PIGEONS

[*Proceedings of the Zoological Society*, 1896]

Mr W. Bateson exhibited three common blue Antwerp pigeons, lent by Mr F. Doggett, of Cambridge, showing webbing between the toes. The amount of webbing differed in each case. All the birds were the offspring of a single pair which were absolutely normal. The following remarks gave the details of each case:

I. *Right foot.* Digits 2 and 3 united by a web extending nearly to end of 2nd phalanx of each toe. In digits 3 and 4 the web does not extend quite so far.

Left foot. Like right foot, but the edge of the web between digits 2 and 3, when the foot is extended, stretches more nearly in a straight line from digit to digit, instead of being curved to form a bay.

II. *Right foot.* Digits 3 and 4 webbed like 2 and 3 in right foot of foregoing. Digits 2 and 3 not webbed at all.

Left foot. Like the right, but the web between digits 3 and 4 extends rather beyond 2nd phalanx and is continued up the side of the toes on to the terminal phalanx as a narrow flap of skin.

III. Both feet have the three digits completely webbed together to the bases of the claws. Right foot has digits 3 and 4 united by a loose web, but digits 2 and 3 are closely webbed together, so that they can scarcely be moved independently. In the left foot all three digits are thus closely united and the foot has a somewhat deformed appearance. The bird can, however, sit on a perch without difficulty.

The hallux is normal in every case.

The web is pink, healthy-looking skin, with scaling on the dorsal surface near the digits.

The birds I and III belong to one nest, but II belongs to a later nest. Mr Doggett states that he had seen one or both birds with more or less webbing in four different pairs of young reared by the same parents. Figures showing the right foot of III and the left foot of II appear, together with a descriptive note by Mr Tegetmeier, in the *Field*, 1896, Vol. lxxxviii, p. 464.

Attention was called to the fact that it is *not* the same pair of digits which are the most webbed in all cases; for in both feet of II the web was developed chiefly between digits 3 and 4, while in I the greatest development was between digits 2 and 3.

PROGRESS IN THE STUDY OF VARIATION, I

[*Science Progress*, I, 1897]

THAT variation is a subject worthy of study for its own sake is becoming recognised, and the numbers of naturalists who are devoting themselves to this study steadily increases. Probably, however, if the nature of the observations required were more generally understood progress would be much more rapid.

The first object of the study is to throw light on the origin of species. An exact knowledge of the facts of variation concerns many departments of biology, but it is in their bearing on the origin and nature of specific distinctness that these facts have their most direct and most manifest importance. It is, then, essential that the subjects chosen for investigation should be such as may be supposed to have this bearing.

Elsewhere (2) I have argued that it is reasonable to suppose that variations of a discontinuous nature may play a preponderating part in the constitution of new species, inasmuch as individuals presenting discontinuous variation in any character differ already from the normal of their own species—in respect of that character—much as one species differs from another.

For various reasons many have taken exception to this suggestion, and though I do not now propose to enter with any detail into matters of theory, nevertheless it may be well to note the fallacy of one line of reasoning upon which objectors have especially relied. It is said for example that discontinuous variation is an exceptional phenomenon, that "sports" are so rare that they may be neglected, and that the appearance of discontinuous variation often seen in collected series of specimens is due to an arbitrary system of collection. These objections are founded partly on an imperfect understanding of the suggestion that discontinuous variation may be a chief factor in evolution, but far more often they proceed from a want of familiarity with the class of facts upon which the suggestion is based.

First, it is evident that there is considerable misapprehension as to the sense in which the term discontinuity is used in its application to variation. Discontinuous variation is carelessly supposed by some to be synonymous with "sport." While however a sport is a dis-

continuous variation it is not in this restricted sense that the term should be used. The word "sport" is generally used to denote a variation connected with the normal by no intermediate individuals. In many—perhaps in most—cases of discontinuous variation there is a complete series of intergrading individuals, not necessarily in each direct line of descent, but occurring among the varying population. Discontinuity in variation is a term of degree. A variation is discontinuous *in proportion as* intermediates between the variety and the type are comparatively infrequent. For a variation is discontinuous if, when all the individuals of the population are breeding freely together, there is not simple regression to one mean form, but a sensible preponderance of the variety over the intermediates. When such a population is seriated in respect of the varying character for statistical study in the manner with which naturalists have been familiarised by the writings of Galton and others the curve of variation has not one peak as in a monomorphic species, but has at least two peaks. The essential feature of a discontinuous variation is therefore that, be the cause what it may, there is not complete blending between variety and type. The variety persists and is not "swamped by intercrossing."

While the word "sport" is expressly used to denote something rare or monstrous, no such idea necessarily attaches to discontinuous variation. When in a species commonly known to us as a constant and comparatively invariable form, an individual is found showing a striking variation, we call it a sport. Thus the six-rayed *Sarsia* ((2), p. 424) is a sport. But in some Medusæ the presence of individuals exhibiting similar meristic variations, either regular or irregular, is so frequent that these "sports" are a normal constituent in any sample[1]. If in England a specimen of *Argynnis adippe* were captured having the silver spots on the underside of the hind-wing absent we should call it an extraordinary sport; but in many Southern localities such specimens are common both in *A. adippe* and *A. niobe*. In the latter species in fact it is the silver-spotted form which is exceptional in many localities.

In any extended view of variation it is soon apparent that a variety which in one species and one locality is exceptional, may in another species or another locality be of constant occurrence.

[1] For example *Aurelia*, see Browne, *Q.J.M.S.* XXVIII, p. 245; various authors *Nature*, 1894; *Zool. Cblt.* II, p. 37, etc., and *Eucope*, Agassiz and Woodworth, *Harv. Bull.* Nov. 1896, p. 121.

So also in regard to the reiterated assertion that the appearance of discontinuity between type and variety is due to the arbitrary rejection of intermediate forms. It is true enough that in very few cases are proper statistics forthcoming, and that as yet it is impossible to say *how much* discontinuity exists in any but a few examples. Nevertheless the fact that in innumerable cases the type is common, and a variety is common relatively to the intermediate forms is familiarly known to collectors. Everything depends on the species and the variety chosen for illustration. For example, in the moth *Callimorpha hera* the hind-wings are generally red, but a yellow variety is common. In this species it happens that specimens of intermediate tints shading through orange and buff are frequent. So far as I know it has not been established statistically that the intermediates are less common than the yellow variety, and possibly enough they are more common. But in *Thais medesicaste* the discontinuity between the type and the variety *honoratii* found flying with it at Dinge, in which the yellow of several cells is replaced by red, cannot be questioned. The intermediate forms are either absent or quite exceptional, though type and variety occur together[1].

The further we proceed in the study of variation the clearer it becomes that we have no warrant for applying the conclusions as to variation and inheritance derived from the examination of one species or one character to the problems presented by other species or other characters. The properties of species are in brief *specific*, as the properties of chemical substances are; and as the properties of each chemical substance have to be separately determined, so must the specific properties of each species be the subject of separate and special study. In what may be called the Chemistry of Species we are far indeed from the era of generalisation.

Discontinuity in variation is in great numbers of cases an observed fact, while the supposition that when organisms are freely breeding together in the state of nature all the varieties they display in size, colour, structure, and so forth, are capable of freely blending, and that the offspring of dissimilar parents tend always to regress to one mean form, is not borne out by the facts. Whether continuity or discontinuity is found depends on the species studied and the character selected for investigation. There is continuous variation,

[1] In illustration of the want of blending in this case it may be mentioned that a specimen was reared by Standfuss ((8), p. 319) which was *honoratii* on the right side and *medesicaste* on the left.

but there is discontinuous variation also. To discover by statistical investigation the degree of continuity or discontinuity which in each species is manifested by the variation of each character is the first business of the student of evolution.

Those who do not admit the probability that discontinuous variation may have a preponderating influence in the establishment of new species will remember that this is confessedly a matter for individual judgment, and whatever views may be entertained on this matter the fact that discontinuity is frequent in variation remains indisputable. Indeed, if it is admitted that the problem of evolution is to be attacked by the study of variation no assumption need be made to justify the prerogative claims of cases in which there is an appearance of discontinuity: for discontinuous varieties have, *primâ facie*, already something of specific distinctness, and whether they are or are not those nascent species we are all seeking, they at least look more like them than other varieties do.

We are in a preliminary stage, and apart even from any question of continuity or discontinuity it is surely well that those who are contemplating systematic investigation of the problem of species should begin by the study of such cases as these. It is, in short, reasonable that the study of variation should be begun with the systematic study of varieties.

By disregard of this limitation a greater scope for statistical refinement may be rendered possible—for the observer is thus free to choose the subject most amenable to such treatment—but it may be questioned whether the compensation is adequate, and whether the solution of the particular problem of the nature and origin of specific differences is greatly promoted thereby.

With this limitation, however, begins a real difficulty, one that it must be feared will for long beset the serious study of evolution. In order even to choose subjects for his inquiry, still more in order to pursue them, the student of evolution needs the peculiar knowledge and experience—the whole apparatus, in fact—which only the collector possesses. In all this he is too often deficient. It is much if the very names of common objects of natural history are familiar to him, and the world of "good species" and "bad species" is unknown. Seldom even can the two classes of men greatly help each other. The collector finds the evolutionist ignorant of what he regards as the rudiments; he only vaguely perceives the other's purposes and is not greatly interested in them. His collection was made with different

objects altogether, and though with the best will in the world he puts it at the service of any one who will work at it, he cannot make it serve a purpose for which it was not designed. The other leaves disappointed. His questions are mostly unanswered, and he is tempted to feel that the methods of the collector are narrow and that he has missed his opportunities. Now both men are right. The future is with the evolutionist, but it is the collector who has made it possible for him to begin his work.

The time has surely come for some attempt at closer collaboration between these two classes of students. Collecting in the ordinary sense, amassing once more the specimens of each species and variety in thoroughly familiar ground, such as England and Central Europe, is a well-worn pursuit from which little novelty can be hoped. Such collecting is little better than a pastime, a thing of momentary value. On the other hand, by only a slight modification in his practice the collector could make his collection a body of evidence of high scientific value, evidence which if we are to progress with the problem of species has become a necessity. Not the less will he find in his work the peculiar fascination which collecting exercises over so many minds.

What the evolutionist asks of the collector is simple. It is, in brief, that he will give to the collection and observation of a few—and for choice, variable—species, the time and effort that he now devotes to the bringing together of rarities. This is a very simple thing, but I believe that at this moment it is a work which scarcely any one has in hand. Scattered over the world there are hundreds of people employing their energies and exercising a high degree of skill in the collection of natural objects and in breeding specimens for their cabinets. If only a few of these had set to work in the way required, we should perhaps already know a good deal about the origin of species.

The fancy is common that in order to investigate evolution, experiments of an elaborate character, dealing with the causes of variation and other recondite subjects, are essential. This is a complete mistake. The first requirement is to know the plain facts as to the occurrence of species and their varieties in the state of nature. To pursue the question of the interrelations of these forms and the degree to which characters are inherited, artificial breeding must of course be undertaken; but even such breeding involves in some cases little more than what many of the best collectors—lepidopterists at all events—are already undertaking for the sake of rearing perfect specimens.

It may be remarked that variation is conspicuously a subject which can be studied by simple means. Since, moreover, it is essential that each observation should be made repeatedly by different observers in different localities, for a long time no one need fear that he is uselessly traversing exhausted ground. We are still at the very beginning.

In what follows I purpose to take a few examples, most of them easily accessible, in illustration of the work in view, hoping that those who propose to devote themselves to such questions may be thereby assisted in the choice of a subject, and that these illustrations may afford some indication of the methods which are required. While specialists will already be familiar with most of the subjects chosen, to students of evolution there will be nothing novel in the statement of method.

Variations so definite as to suggest that they may possess something of specific distinctness may roughly be divided into two classes. In the one the variety is found associated with the type, mingling and, we must suppose, breeding freely with it; in the other the variety is found partly or entirely separate from the type. It is perhaps especially in dealing with cases belonging to the second category that we stand in the greatest need of the co-operation of the general collector; but in order to explain more clearly the particular treatment which is needed in cases of the second class, two examples of the first and simpler kind may be conveniently spoken of.

The first is an example of variation familiar to all entomologists, that of *Amphidasys betularia* L. and its variety *doubledayaria*, Millière. The typical form is the well-known peppered moth, a large insect having the whole upper surface of the wings of a white ground colour, almost uniformly speckled with black. The sexes are similar. Of this insect a unicolorous *black* form, the variety *doubledayaria*, is now commonly distributed over the northern and midland areas of England. The special interest of this case lies in the fact that it is one of the few examples in which a variety is known to have come into prominence within recent times. Though the case is notorious in entomological circles its importance has scarcely been recognised by evolutionists. A short summary of the evidence is given by Barrett (1), see also Chappell (3). Briefly the facts are that this striking black variety, of which the early entomologists say nothing, was first met with as a rarity in the North of England towards the end of the

'forties. It was figured and named by Millière (6) from an English specimen. The variety lives on the various food plants of the type. In 1865 it is reported that most of the males attracted by females exposed at Manchester were of this dark form. In a few years it had spread through a great part of the Midlands. In 1870 the black form was almost as frequent as the type at Newport, Monmouthshire, and a few years later the typical form had almost entirely vanished from that district. At Chester none but black specimens have been met with for many years. In recent years casual specimens have been taken in various English localities as far south as Berkshire. On the Continent the appearance of the black variety was much more recent. A dark specimen—though not so dark as *doubledayaria*—was recorded in Belgium in 1886 (5), and again intermediates are reported from Belgium in 1894 (5). In the past ten years the black form has spread over a great part of Germany, as far as Silesia and Dresden ((8), p. 316).

Here then is an actual case of the establishment of a natural variety. If only the Lancashire entomologists had put by 100, or even 20, specimens of *betularia* taken at random year by year, what a splendid record it might have been! But though there is no such complete evidence as this, the leading fact is clear. In a short time, some 50 years, a dark form has supervened on the light one. Now did this come about by the gradual shifting of the average form through all stages of grey to black? It is practically certain that it did not. The change came about by the success of a particular dark strain or strains. Not that it must be supposed that intermediates are unknown. On the contrary, Mr Barrett, who kindly showed me several of them, tells me that he believes that they were formerly more common than they are now. Moreover, in Belgium it seems clear that an intermediate strain has established itself, and intermediates are also said to be plentiful in the Rhenish Provinces and Westphalia, together with totally black forms. In some parts of this district, however, as in Barmen and Crefeld, the typical *doubledayaria* is said to be already the commonest form (8). But there is no doubt both that the totally black form existed at an early stage in the transformation side by side with the light one, and that in localities where both occur the same is still the case. The course has not been that the insects of each successive district have become more and more tinged with black, till they culminated in *doubledayaria*, but rather that *doubledayaria*, or less often one of the intermediate forms, spread

into, or at least appeared in the area, and either coexists with the type or has replaced it.

There is great need for experimental and quantitative evidence as to the inheritance in crossed and thoroughbred strains, and the subject is probably well suited to such work. Nevertheless the results of the few experiments that have been made are in accordance with the expectation based on the simultaneous occurrence of the forms in nature, that there is imperfect blending between type and variety, for Steinert (9) raised from a typical black wild female found at Dresden a brood consisting of 75 *betularia* and 90 *doubledayaria*. Two of the *betularia* were slightly darker than the normal form.

Similar changes are said to be taking place in several other British species of Geometræ, but the evidence seems to be less clear and less extensive than it is in the case of *betularia*.

Here, then, we have the means not merely of studying the relations of variety to type, but also of actually witnessing a case of evolutive change. If some one will make it his business to collect samples of *betularia* from various districts he will certainly make a valuable contribution to the science of evolution. All that is needed is that wild samples should be taken at random, fairly illustrative of the population of each district, and sorted into classes, (1) normal *betularia*, (2) light intermediates, (3) intermediates, (4) dark intermediates, (5) typical *doubledayaria*. A simple way by which something might be done would be to arrange year by year for the exposure of a few fresh females reared in captivity, when the attracted males could be taken in the way often followed with such species. This would of course only give information as to the male population, but that would go far towards answering the question.

The numbers which it would be desirable to collect in each sample should of course be as large as possible, but there is a tendency among those not practically acquainted with such problems to greatly exaggerate the need for excessive numbers. To rightly assess the importance of minute and insensible variations, doubtless vast numbers of individuals are needed, but in cases like that of *betularia* probably a very moderate number would in the first instance suffice to give a broad but reliable indication of the facts. If in 100 specimens[1] there were 30 dark and 10 intermediate, the subsequent

[1] It is assumed, of course, that the specimens are collected in such a way as to preclude the possibility that they are all one family.

collection of 1000 would probably change the absolute percentages a little, but it is unlikely that it would materially modify any conclusion based on the first sample.

No doubt in districts where the variety was very scarce large numbers would be needed, and it is doubtful whether such cases are suitable for statistical investigation. In the Cambridge district, for instance, *doubledayaria* is still almost unknown. In addition to a typical specimen of the variety I lately took, I can learn of only two others, which were taken severally some years ago. The ordinary form, however, is common, and it is likely that a few hundred specimens would contain no *doubledayaria* at all.

In order to follow up the statistical study of wild specimens and to obtain experimental proof of the modes of transmission of the varying characters by artificial breeding, a wider range of observation is necessary, and, from a few experiments only, contradictory results are almost sure to follow.

The difficulty arises especially from the fact that the power of transmission of the individual is undoubtedly affected by its own back-breeding, a quantity for the most part unknown. In illustration of this I may refer to the discrepancy between the results obtained by Burckhardt, referred to by Standfuss ((8), p. 307), in crossing the varieties of *Spilosoma lubricipeda* and the results obtained by several observers in this country working with the same species. It is well known to entomologists that of this species there is a peculiar dark form, *zatima* Cram., found in Heligoland[1].

This variety has been observed to breed true when paired (7). Now there is good evidence that when the Heligoland variety is crossed with the type, the offspring may consist of the type of true *zatima*, and of certain lighter forms of this variety, named var. *intermedia* of Bang-Haas. But between this latter variety and the type, though crosses of the most various nature were continued for four years and an immense series of specimens reared, the intermediates were always wanting (8). But this is not because such intermediates cannot exist. In England a dark race of *lubricipeda* has been artificially reared by selection (starting from naturally dark specimens) by the Yorkshire entomologists, which approaches rather nearly to the true *zatima*. These artificially produced forms are known as *radiata*. In a series of them belonging to Mr Porritt's strain, kindly

[1] Whether it is there associated with the type or not I cannot find clearly stated by any authority, but I gather that the normal as well as the variety occurs in the island.

shown me by Mr Barrett, are many of both sexes which quite fill up the gap between *intermedia* and true *lubricipeda*. Still more completely is this interval filled by a series lent me by Mr W. H. B. Fletcher, which had been reared by crossing the partially artificial *radiata* with another variety.

Again Standfuss records that by crossing the natural dark variety *eremita*, a form of *Psilura monacha*, with the type, a brood was produced containing one female *eremita*, the rest being all typical *monacha*. This cross-bred female he again crossed with a male of the type and there resulted twenty-two normal *monacha*, twenty-three typical *eremita*, and six individuals in which the characters of type and variety were *asymmetrically* mixed. Such a brood is a clear proof of imperfect blending of the two characters. But Mr Fletcher by starting with a normal female *monacha* raised by selection among her offspring, successively repeated for five years, a series of which a few in the latter years are practically *eremita*, and in this series numerous intermediates occur.

In each case the indication is the same, that the results depend on the strain employed. It is greatly to be hoped that these experiments may be repeated and detailed statistics of the results published.

So far as I can learn those that have been hitherto performed have not been for the most part recorded in any detail and the specimens have been largely dispersed.

The other case which I shall take in illustration of a similar phenomenon is that of the hairy and smooth forms of the Cruciferous plant, *Biscutella lævigata*. I have had opportunities of observing this plant in several localities in the wild state, and in a recent communication to the Royal Society Miss E. R. Saunders has given the results of experimental cultivation and artificial fertilisation of its varieties. The facts are these. The plant is a common Alpine species with a rather wide distribution. Some authorities describe it as hairy, others as glabrous. Generally it is stated that it may be either hairy or glabrous. The essential fact to the student of variation is that in certain localities the hairy and the glabrous forms may occur side by side in the same meadow or on the same rock. In my experience the hairy form is the commoner. The plant is common, for instance, in the Val d'Anniviers, at Bérisal, near Airolo, and elsewhere, exclusively in the hairy form. The leaves and stems are thickly covered with a short pubescence, varying in texture, but commonly the hairs

are stiff. But in the Val Formazza, side by side with the hairy plants, are others exactly resembling them in the rest of their structure, but having the surfaces of the leaves and stems smooth and devoid of hairs. In the great majority of these smooth-leaved plants, however, the margins of the leaves and the leaf-teeth, often also the mid-rib, bear hairs: it is the *surfaces* which are smooth. In this valley, both above and below the Tosa Falls, the plant abounds in both these two forms, the smooth being on the whole the more abundant. Now between these two there are various intermediate forms making a complete series connecting them. But though the degree of hairiness varies, and the degree of smoothness varies, the immense majority of plants in the locality can be referred unhesitatingly either to the hairy class or to the smooth. Plants which are so intermediate in character as to cause the observer any doubt as to the class to which they belong are decidedly scarce. Owing to the fact that the plants increase much by runners, forming new crowns which afterwards separate, it is impossible to say which should be counted as "individuals," and hence it is not easy to see how a reliable numerical measure of the discontinuity can be obtained, but that the fact is substantially as stated there is no doubt.

The question then arises, how is it that these two distinct varieties can exist side by side, exposed to the visits of insects, without regressing to the mean form, which, as was stated, is comparatively scarce? To determine this Miss Saunders made artificial crossings of the two varieties in the Cambridge Botanic Gardens. The mongrel seedlings, judged by their first few leaves, consisted of some hairy, some smooth, and a large number of various intermediate forms. But it was found that as these seedlings grew older, while the hairy continued to put up leaves which were hairy, the intermediates in their later leaves turned to smooths. The original smooths also to some extent became smoother. When, therefore, the well-grown mongrel plants are examined they present just the same appearance of discontinuity which the wild plants at the Tosa Falls do. This discontinuity is, therefore, the outward sign of the fact that in heredity the two characters of smoothness and hairiness do not completely blend, and the offspring do not regress to one mean form, but to two distinct forms. The variety, in short, is not "swamped by intercrossing."

Which may be the older form we will not venture to discuss. It is, however, of no small interest to note that Miss Saunders found that

the smooth plants suffered far more from slugs—which attack the species greedily—than the hairy ones did. We have no information on the point, but it is just possible that some creature which elsewhere eats off all the smooth seedlings is absent from the Val Formazza. The eggs of *Pieris napi* are laid on both kinds, and the larvæ can eat both kinds, but whether they prefer either I cannot say.

These two cases must suffice as examples of those varieties which, coexisting with the type, have the quality of distinctness. Many such cases will be known to those who collect animals or plants. Of few indeed have any satisfactory accounts, much less statistical records, been prepared showing how or in what proportions the various forms occur in nature; and in still fewer has any cross-breeding been systematically carried out. In most cases all that we know is the bare fact that such a species has such a variety commonly or occasionally found associated with it, if so much. Rarely do we know for certain whether intermediate forms exist or not. On such points the writings of systematists are too often consulted in vain.

In all these cases the course to be followed in the first instance is simple, and consists in examining and, if possible, preserving a fairly numerous sample taken at random from as many distinct localities as possible. In recording the results of such collecting, the essential points to be noted are these:

(1) That the variety occurs associated with the type; that it is scarce or abundant.

(2) Whether the variety is connected with the type by a series of intermediate forms or not.

(3) If intermediates do occur, it is then to be determined whether in each sample the specimens can for the most part be readily sorted into type and variety, or whether specimens that are so intermediate as not to be thus referable are common.

(4) The above questions to be answered separately for each sample from a distinct locality.

With regard to the third point, it is obvious that whenever it is possible the numerical proportions which the type, the variety, and the intermediates bear to each other should be determined carefully by statistical seriation. This must be done in suitable cases by measurement, and in other cases by the constitution of a series of grades and counting the specimens belonging to each grade. But even where by the intrinsic circumstances of the case or by the conditions under

which the collecting or observations have to be conducted, numerical estimations cannot be made, it is certain that most valuable material would be provided merely by answers to the first two questions, with a careful statement of impression as to the third point. These answers would not merely show roughly whether the case was likely to repay further and special investigation, but they would provide that general outline of the properties of species in regard to variation which all the labours of the systematists have failed to provide, though it has become an urgent necessity to progress. The systematists have given us a catalogue of the material, treating it from the cataloguer's standpoint, but in the light of the study of variation we are still at the first recension.

In a subsequent part the application of these methods to the special problems presented by local races will be considered.

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PROGRESS IN THE STUDY OF VARIATION, II

[*Science Progress*, II, 1898]

We have now to examine the special case of local varieties or races, and to consider how the phenomena they present may best be turned to account in the attempt to investigate objectively the origin of species. It is here that we are especially dependent on the efforts of the collectors. Without great collections little progress can be made, but by modification of the usual practice their utility for the solution of these problems might be much increased.

It is a fact familiar to every naturalist that in very many species individuals living in different areas are dissimilar, and that by these dissimilarities the species may be broken up into local races. This phenomenon of local differentiation is so common that species in which it is not in some degree apparent may almost be regarded as exceptional. The differences may be exceedingly slight, and appreciable only to a person who has had long experience of the form in question; or, on the other hand, they may be so decided that it is only after special study and examination of series of specimens from many localities that the local races can be recognised as belonging to the same species.

In addition, too, to cases of this latter order, in which reason has been found for uniting dissimilar local races, there are numberless instances in nearly all orders of animals and plants where it is practically certain that forms which on account of their dissimilarity and distribution have been considered as distinct, might with almost equal propriety be regarded as local races of the same species. Local differentiations of this kind are the despair of the systematist. How may species be distinguished from local forms? How great must the differences be, and in what organs must they appear, to justify the constitution of a species? On these weary questions volumes of controversy have been spent. No general rule can be found, for no real distinction exists, and in practice each man must follow his own standard. So long, however, as each distinct form receives a separate name by which it can be known and treated of it matters perhaps little whether it is reckoned as a species, sub-species, "representative species," local race or variety. All that we have to remember is that these various terms have no precise signification.

The existence of such local forms is nevertheless one of the best possible points of departure for an attempt to study the origin of species. In each case, where two local varieties are known, the problem of the origin of species is presented in a *particular* form. How did those two particular varieties A and B come into existence?

Causes apart, by what steps in descent was the one produced from the other, or both from something else? These are nascent species if there are any on the earth. Here if anywhere is our chance to see, if not the mode by which species come into existence, at least the way in which differentiated forms are connected together, and the steps by which they may separate. It is true enough that even in the case of most local races which are materially distinct the evidence as to the connecting steps is gone. In one locality one form is found, in another locality another form. Each area is distinct and isolated, and has its distinct population; beyond that nothing is known. But besides these there are other cases, rarer perhaps, but still fairly numerous, in which local forms inhabit conterminous areas, and, though distinct enough in their chief habitats, yet meet each other and breed together in the intervening district, producing offspring which we have no reason to suppose infertile. Such cases have a prerogative claim on the notice of the evolutionist. Two forms, each well defined, each, as is presumed, adapted by its peculiarities to its own area, meet in an intervening area. In what state is that intervening population? On seriation does it appear that the population consists mainly of one normal form, the mean between the two others, or is the intervening population found to be practically divisible into two groups of individuals, the one more like the one race, and the other group more like the other race? In any such case there is in fact an opportunity of seeing "swamping" by intercrossing, of getting evidence as to whether the two races are capable of freely blending, or whether there is any discontinuity between them.

In regard to some of the more familiar examples, certain of which are spoken of below, discussion has arisen on the question whether the population occupying the intermediate area where the two races intergrade should be regarded as hybrids between the two, or rather as a still undifferentiated population. A third possibility is that the one race is being or has been directly formed from the other by discontinuous variation, and that in the area of intergradation the process is going on. On consideration, however, it will be seen that,

whichever be the true account, the discussion must be a barren one; for if there is discontinuity between the two forms, whether the two races are newly met or newly dividing the appearances would at any one point of time be the same. This question, like so many others concerning evolution, could only be answered by appeal to observations made at several moments separated by intervals of time. Such evidence is, of course, wanting. Nevertheless, for our purpose a knowledge of the truth of one or other of these views is not immediately needed. The essential fact is that the two forms, though distinct enough to pass for separate species, did they not occupy the same area, on overlapping interbreed in nature. Though in the ordinary sense of the term forms are not "species," yet they have many of the attributes of species.

If it is true that the evolution of the one form from the other, or of both from something else, has proceeded by a long series of insensible steps, of which each in turn has been a normal in its own day, surely we should expect to find the intermediate area occupied by an intermediate population, having an intermediate (if not the mean) for its normal. More especially should we expect to find this state of things in those instances in which the two local races are what are called climatic varieties, varieties that is to say associated with conditions which we can recognise as distinct (without postulating any direct relation of cause and effect). It is not rare, for instance, to find a species represented in the North by a northern race, and in the South by a southern race. In such a case, if the two forms inhabit a continental area, divided by no natural barrier, we should expect, on the hypothesis indicated, that in the intermediate area there should be an intermediate normal. Or, more precisely, we should expect in travelling from North to South to pass through country inhabited by a whole series of normals, passing in unbroken continuity from the distinctly northern form to the distinctly southern.

Again, if a lowland species is represented in the mountains by an Alpine race we should expect as we travel up the valleys to pass through a series of normals, each appropriate to its own level. We may concede that a full chain of intermediates as normals need not be expected in every case, but that the state of things ought, on the whole, to bear out this expectation is surely clear, and if the hypothesis of an essentially gradual evolution is true, the geographical transition from the one race to the other should be essentially a gradual transition.

It is very likely that cases could be produced where such essentially gradual transitions occur, but, as will be shown, there are others which cannot readily be so described. Whether there are any general features distinguishing the two classes of cases we cannot yet say. It is the object of these remarks to call attention to the paramount importance of such phenomena as subjects for investigation.

Few indeed are the instances which we can yet with confidence refer to either class. Collectors and systematists have hitherto been content as a rule with the bare knowledge that there is sometimes intergradation between local races. Statistical evidence of the modes of intergradation are almost entirely wanting. Commonly the information is of the most meagre description; and even in the case of easily accessible forms no collections or experiments have yet been made with a view to answering a question of such peculiar interest to the evolutionist.

In the following pages I propose to take a few illustrations—most of them already well known to specialists—showing the kind of phenomena which are thus open to observation. The methods that should be applied are essentially the same in each case, consisting in:

(1) The collection of large samples taken at random in the area believed to be occupied by the pure races.

(2) Separate seriation of the individuals of each sample according to the degree in which the differentiating character is presented.

(3) Similar collection and seriation of similar samples from a series of stations connecting the areas occupied by the pure races.

(4) In suitable cases experimental crosses between the pure forms and between each pure form and such intermediates as can be obtained.

It is unnecessary to say that in planning observations on these lines, special regard must be paid to the possibilities of error due to migrations and other sources of error affecting particular cases.

Local races may be distinguished by differentiation in respect of various bodily features, though naturally the most familiar are those which are distinguished by some conspicuous and easily recognised characteristic, such as peculiar stature or proportions, colour, sculpture, and so forth. But there are several well-known instances where intergradation occurs between races distinguished from each other by what are called "anatomical" characters. A good instance

of such a phenomenon is that of a species of *Cistudo* in N. America, which is represented in New England by a form with four toes on the hind foot, while Mexican representatives have three. This form was originally considered by Gray as a separate genus, afterwards as a separate species. Subsequent evidence has shown that the fourth toe fades away so gradually that the two forms are clearly one species. Specimens have also been seen with three toes on one foot and four on the other[1]. These animals are so common that a statistical study of their variation in nature should not be very difficult to make.

Among birds some of the most striking examples are known, and have been the subject of a good deal of discussion which, for the most part, has followed exclusively the lines indicated above. One of the best known is that of the species of *Colaptes* (a woodpecker) inhabiting the United States and Mexico. In this instance the facts have been examined in considerable detail, especially by J. A. Allen (1), who has given a careful summary of the evidence derived from the study of a large mass of material. As appears from his observations the case is briefly this. Omitting forms with more restricted range, two species of *Colaptes*, *C. auratus* and *C. cafer*, occupy nearly the whole of N. America. A band of country 300 to 400 miles wide extending from British Columbia to Texas is common to the two forms. North and East of this belt *C. auratus* is found unmixed, while *C. cafer* in the pure form occupies most of the country south and west of the common area. The distinctive characters are very striking, the most noticeable being the following:

C. auratus.	*C. cafer.*
1. Quills yellow.	1. Quills red.
2. Male with black malar stripe.	2. Male with scarlet malar stripe.
3. A scarlet nuchal crescent in both sexes.	3. No nuchal crescent in either sex.

Besides these there are several less conspicuous differences, one of the most singular being due to the fact that the colours of the crown and throat are *transposed* in the two forms, *C. auratus* having a grey crown and a brown throat, while *C. cafer* has a brown crown and a grey throat.

In describing the "ever-varying combinations" of these characters found in the area where the races overlap Allen states that the specimens range from individuals which show the characters of one race

[1] I have referred to the evidence in detail, *Materials*, No. 609.

with only a trace of the other to birds in which the two sets of characters are about equally blended:

> Thus we may have *C. auratus* with merely a few red feathers in the black malar stripe[1], or with the quills merely slightly flushed with orange, or *C. cafer* with either merely a few black feathers in the red malar stripe, or a few red feathers at the sides of the nape, or an incipient, barely traceable scarlet nuchal crescent.... The quills may be orange yellow or orange red, or of any shade between yellow and red, with the other features of the two birds about equally blended. But such examples are exceptional, an unsymmetrical blending being the rule, the two sides of the same bird being often unlike. The quills of the tail, for example, may be part red and part yellow, the number of yellow or red feathers varying in different individuals, and very often in the opposite sides of the tail in the same bird. The same irregularity occurs also, but apparently less frequently, in the quills of the wings. ...A bird may have the general coloration of true *cafer* combined with a well-developed nuchal crescent, or nearly pure *auratus* with the red malar stripes of *cafer*.... Or we may have the general plumage as in *cafer* with the throat and crown as in *auratus*, and the malar stripe either red or black, or mixed red and black, and so on in almost endless variations, it being rare to find, even in birds from the same nest, two individuals alike in all their features of coloration.

Now, though from this account it appears that the several characters may combine in varying ways, the great irregularity and especially the asymmetry of the combinations are strong indications that there is not free blending of the characters, but rather that though they may coexist in the same individual they are in some degree alternative, forming, in fact, a kind of patchwork. Though even in this—one of the best known cases—adequate statistics are still wanting, it seems to be clear that there is no great population with either the mean or any other intermediate form as a definite normal.

A more complex example is provided by species of the genus *Quiscalus*, the boat tail grackle of N. America. The facts are indeed so complicated that they cannot be represented in a brief statement. A full account of this matter is given by F. M. Chapman (2) who has made, as far as his material permitted, a statistical tabulation of results. Here again the variation is in colour of plumage, which may take various dark metallic shades not easily described in words.

[1] A Californian specimen in the Cambridge Museum shows these feathers partly black and partly red. Each feather though black in its basal parts has a red tip, the black pigment being apparently transmuted into red pigment.

Concomitant variation in size and proportions are also shown to occur. The facts as stated by Chapman are, broadly speaking, that *Quiscalus œneus* has a breeding area from the Rio Grande Valley northwards to British America, and north-eastwards to New Brunswick. In the area south-east of this *Q. quiscula* occurs, ranging from Florida to Massachusetts. In Pennsylvania and Massachusetts (probably also in a belt of country extending south-west from Massachusetts through Pennsylvania to the north of the Mississippi) the two forms meet and intergrade. In the rest of its range *Q. œneus* is remarkably constant. The complexity arises from the fact that *Q. quiscula* occurs in a variety of forms which can be regarded as three phases of coloration. Phase No. 1 is found in S. Florida associated with Phase No. 2, and many intermediate forms. At the north of its distribution Phase No. 1 is absent, No. 3 being there chiefly found, associated with No. 2 and all intermediates. In the central part of its range all three phases and intermediates occur together. The transition from *œneus* to *quiscula* occurs exclusively through Phase No. 3 of the latter.

From the particulars given it seems likely that though the transition is gradual in the sense that all intermediates occur, being indeed frequent in the area of intergradation, yet here again the connecting links are not a series of normals following each other in succession along lines passing from the area of one race to that of the other. Another example well known to ornithologists is that of the rollers, *Coracias indicus* and *affinis* (see Dresser (3) and Sharpe (5)). Here again the coloration of the two races or species is quite distinct. *C. indicus* inhabits the Indian Peninsula generally, extending westwards to Asia Minor, while *C. affinis* belongs to British Burmah and Indo-China. It spreads, however, westwards to the neighbourhood of Calcutta and onward to Sikkim and Nepal. This part of its distribution is common to the two forms, and intergrading occurs. A considerable series of intermediates from this region is preserved in the British Museum, and from these and others described by Dresser it appears that here again there is no definite race of intermediates grouped round the mean as a normal, but that the intermediates are a heterogeneous body, and highly variable. It is quite possible that on seriation they would be found to be on the whole divisible into two groups favouring the two types respectively.

Birds, however, are not well adapted to statistical treatment of the kind contemplated. Their large size, frequently migratory habits, and the comparative difficulty in preserving them in large numbers make

them for the most part unpromising material for such work. Besides this, it is in very exceptional cases only that they can be bred in captivity. Before passing to other examples, however, it may be noted that in these cases, though the individual parentage of the intermediates or of the types in the area of intergradation is scarcely as yet a matter of observation, there is nothing in the facts inconsistent with the possibility that the whole phenomenon may be one of discontinuous variation. Nevertheless, it is quite as possible that the intermediates may in each case be the result of cross-breeding. If the latter is the true view, then, since the whole population is not found to have regressed to the mean form, this state of things must be due either to the existence of some principle by which the types mate more often legitimately than illegitimately, or to the existence of natural discontinuity, or to the unfitness and consequent extermination of the mean forms. The last hypothesis is so improbable that it need scarcely be considered. No support could be produced on behalf of such a view, either from facts of the case or analogy of other cases.

Among Lepidoptera there is perhaps more hope of obtaining direct evidence on this question, and there are numerous cases which would well repay careful work. Scarcely any have been touched as yet.

A remarkable example has been observed by W. H. Edwards (4) among the N. American Papilios. The form known as *P. oregonia* is a species much resembling *machaon* in general coloration. It is found in Washington Territory and British Columbia. Another "species," *P. bairdii*, has the upper surface largely covered with black scales, especially in the female, and in general appearance may be said to resemble the *asterias* group more than the *machaon* group. It occurs in Arizona without intermixture with *oregonia*, just as the latter occurs in the north without intermixture with *bairdii*. However at Glenwood Springs in Colorado *oregonia* and *bairdii* were found flying together by Edwards.

By rearing eggs laid by the Glenwood females, he found that both forms could be reared from females of either form, eggs from *bairdii* females producing both *bairdii* and *oregonia*, and eggs from *oregonia* producing both *oregonia* and *bairdii* (statistics given). The experiments showed that this is not merely a case of seasonal change, both forms occurring in each brood.

For our present purpose it is important to notice the fact to which Edwards calls attention that the *oregonia* and *bairdii* in the locality of intergradation were not for the most part the pure forms as they

occur in areas where there is no intermixture. Some of the *bairdii* were typical, but most departed in different degrees from the type, no two being quite alike. The *oregonia* also departed from the type in the direction of *bairdii*. Nevertheless, as the whole account shows, here there were two well-marked forms like those elsewhere known as local species or races, breeding together in one locality but not regressing to the mean form.

I will now refer briefly to two examples of marked local races, whose relations I have been myself endeavouring to investigate. The cases are those of *Pieris napi* (the green-veined white butterfly) and its Alpine var. *bryoniæ*, and *Pararge egeria* (the speckled wood butterfly) and its northern form *egeriades*. I have been collecting and crossing these species for the past three seasons, and am still far from arriving at definite results, but I mention the subject here in the hope that others may be induced to look out for some of the points to be observed.

As regards these cases the history is far too complex to be treated as a whole in the present paper. Difficulty arises not only from the great extent of country inhabited by the species and their varieties, but also in the case of *napi* from seasonal dimorphism. *P. napi* in this country is too well known to need description. Here as a rule the summer brood do not differ greatly from the spring brood, though exceptionally they may do so. The summer form when it is distinct is called *napææ*. It is chiefly characterised by the large size of the two spots on the fore-wing in the female, and by the great reduction in the amount both of dark venation on the upper surface of the fore-wing, and of green venation on the lower surface of the hind-wing. Such a distinct summer form abounds in the lower parts of the valleys in the Alps and of course in most of the warmer regions of Europe.

At and above 3000 feet or rather less, *bryoniæ* may often be met with in those valleys which descend from the high mountains. It is in the *female* that this variety is clearly marked, being characterised by the presence of bands of brown scales following the nervures or the upper side of both wings, especially in the fore-wing. The male closely resembles the spring male of *napi*, and is not generally, if ever, distinguishable from it with certainty. *Bryoniæ* extends up to 6000 feet. Whether this Alpine form ever occupies any considerable area without *any* admixture of *napi* I do not know. As regards particular hillsides I think it does, but my experience is that colonies of *napi* may occur up to nearly 6000 feet, especially near chalets, appearing in summer broods identical with those of the lowlands.

That in such places the two forms occupy more or less distinct spots is, I think, probable[1]. Lower down, however, *napi* and *bryoniæ* may in many places be taken flying freely together, but in such localities, according to my experience, intermediates are of exceptional occurrence and are less common than the type forms. Why is this?

The case is an interesting one in several ways. Weismann has made this species the subject of a good deal of speculation and some experiment. In his earlier paper (6) he regards it as certain that *bryoniæ* is an ancient form dating from the glacial period and that *napi* has been very gradually evolved from it as temperate conditions supervened. In the later paper (7) from the fact that two male *napi* and a *bryoniæ* female irregularly patched with white emerged from some forced pupæ supposed to be all offspring of *bryoniæ*, he is apparently disposed to doubt his original view, though, as he points out, the *napi* may have been merely introduced larvæ and the blotched specimen may have been gynandromorphous. The possibility that there may be discontinuity is not considered. Moreover, the matter is greatly complicated by the fact that *bryoniæ* is not, as Weismann states, exclusively one brooded, for I have reared summer broods, emerging in August, both from *bryoniæ* females caught at Fobello (3000 feet) and above the Tosa Falls (5500 feet). The former were flying with *napi*, and for anything I know these summer emergences may have had a *napi* father.

Those from Tosa may also have been cross-breds, though this is less likely. All the second brood from Fobello were intermediate and some of those from Tosa are so also, though the rest of the latter are *bryoniæ*. It appears therefore to be possible that the intermediates found wild may be a second brood from *bryoniæ*. In order to determine this it would be necessary at least to have statistics from one locality extending over the whole period during which the species fly.

The view that *napi* has been very slowly evolved from *bryoniæ* or *bryoniæ* from *napi* is not easy to reconcile with the facts of the present occurrence of the forms. *Bryoniæ* is met with in the far North and again in the high Alps. If *napi* has been continuously evolved from it, passing through a long series of intermediates as normals, we should expect that those places in Europe which have a climate intermediate between glacial conditions and temperate conditions would have a

[1] It is possible that the two forms in such cases live on different plants. The chief food of *bryoniæ* at Tosa is *Biscutella lævigata*, but both forms eat many kinds of Cruciferæ, and I cannot find that the colours are changed by difference in food.

normal population of intermediates. On such points the systematic treatises are not very reliable; but I cannot discover that such a population exists anywhere. With regard to Norwegian and Arctic specimens the accounts are somewhat contradictory, and the individuals I have seen are too few to warrant a definite opinion. The same applies to Central Asian forms. Certain it is that in the Alps on passing from the lowlands to alpine conditions a population having an intermediate as its normal form is not met with in June and July. At this time in such localities the common forms are *napi* of the second brood, *bryoniæ*, and occasional intermediates which may be either pure-bred second brood *bryoniæ* or cross-breds, or both.

It is to be hoped that some who have the requisite opportunities will make collections of large samples of these forms, either in the North of Europe or in alpine regions, and so contribute to the solution of this very attractive problem. It will be understood that the account here given is the merest outline of the facts.

It is interesting to reflect that if we had known nothing of the history of the origin of *A. betularia*, var. *doubledayaria*[1], and if we had not actual historical evidence that it has replaced the type in the North of England we should most certainly have been told that the one had been very gradually evolved from the other in the course of ages. The same example shows moreover that there need be no natural distinction between the case of a variety discontinuously occurring with the type and the case of two local races occupying distinct areas. We might suppose that the former case is in reality comparable with familiar examples where there is an apparently constant dimorphism of one sex, or with the reciprocal dimorphism of many flowers, in which it is believed that the dimorphism is a permanent attribute of the species as much as the differentiation of parts in the body of an individual. The case of *betularia* shows how the one may pass into the other.

Before leaving the subject I will give one more example, to which

[1] To the experimental evidence of discontinuity in this case I should have added the following reference, E. R. Bankes, *Ent. Rec.* VII, p. 181. Since the first part of this article was published, Mr W. H. B. Fletcher has kindly lent me the entire brood produced from a black female, reared in captivity, which was tied out at Worthing where only the type is known. There can thus be no doubt she was fertilised by a *betularia* male. The offspring are sharply divided as follows: *betularia*, ten males, eight females; *doubledayaria*, six males, five females. Curiously enough one of the *betularia* is an abnormally light specimen. The rest are either normal, or else completely black all over.

I have been paying some attention, because it is especially one where co-operation is needed. I take this opportunity of thanking M. René Oberthür for kindly sending me specimens, and for other assistance rendered me in regard to this species. The Speckled Wood butterfly of England is now well known to be a geographical variant on the form inhabiting France and Spain generally, the Mediterranean littoral and a great part of the rest of Europe. In the South the pale yellow of our own insect is replaced by a bright fulvous yellow. The southern form is now called by the strict rules of nomenclature *Pararge egeria*, while the British form is the var. *egeriades*. Omitting other complications, our problem is raised in the simplest form by the facts of the distribution of the varieties in the French and Spanish continent. At Gibraltar *egeria* flies alone. Practically similar *egeria* flies alone in the Basses Pyrénées (as also at Avignon and Tarascon) and in all the country northwards as far as Poitiers. About sixty miles north of this point, at Tours in the Loire Valley, country not noticeably different, there is a very different form which is almost exactly intermediate between the two chief varieties. This intermediate form is spread over Brittany and Normandy. Those from the neighbourhood of Paris are of the same intermediate form, or perhaps a little paler. As far as my own observation goes, there are essentially *three* forms, southern, northern and intermediate. From between Poitiers and Tours I have no specimens, and it would be interesting to know whether in that region the southern form shades off into the intermediate. Similarly it would be interesting to have collections from places where the intermediates might be expected to shade off into the northern form.

It is certainly likely that there may here prove to be a true case of continuity, but so far this is not quite clear, either from the wild specimens or from those that have been reared by crossing. The cross between the northern and southern types usually produces the intermediate, agreeing exactly with Breton specimens, but on recrossing these with the southern form my evidence inclines, but by no means certainly, towards the conclusion that there is not complete blending between the two. I anticipate, on the whole, that fuller investigation will show that there is complete or almost complete continuity. The abrupt change on passing from Poitiers to Tours is, however, scarcely consistent with this anticipation.

The insect is very local, and probably wanders hardly at all. It is therefore a good subject for this inquiry. The west side of France is

most suitable ground for the investigation, for here there are no mountain ranges or other barriers.

In mountainous parts of the country the true *egeria* is always replaced by paler forms. Such forms are found, for example, at Chambéry, and these are not strikingly different from those of Brittany, though on the whole inclining to the fulvous type, while from Doubs M. Oberthür has sent me specimens precisely like English ones.

Cases which might repay statistical study in this country are, amongst others, those of the varieties of *Polyommatus agestis* and the two forms of *Fidonia piniaria*. The latter is very probably a case of discontinuity. In examining it difficulty may arise, as Mr Fletcher has pointed out to me, from the possibility that with the recent plantation of the Scotch fir in many parts of the country artificial introductions may have taken place. I should be grateful for the loan of series of specimens or for accurate records of the occurrence of these forms.

The illustrations here given will suffice to show lines on which the objective study of the origin of species may, as it seems to me, be profitably pursued. Until work of this kind has been carried out in many cases, both statistically in the field and by cross-breeding in captivity, we have not got the material even for a preliminary survey of the relations between species and variety. Such work is pre-eminently to be commended to collectors and systematists. It is for want of it that so little progress has been made with these questions. It is depressing to see how those who are engaged in the business of systematic work often neglect to give the essential particulars as to the variability of the material submitted to them for description. That such a character is "variable," or "so variable that no reliance can be placed on it" is often all that we are told, when in many cases with little additional trouble the number of specimens exhibiting each variation could have been recorded, thus greatly lightening the task of those who come after. If collectors and systematists would arrange their work in such a way as to bring out and not conceal the objective phenomena of evolution, and if the evolutionist would appreciate that the proper way to study the relation of type and variety is to take up the work at the place where the systematist leaves it, we should have that partnership between the two classes of naturalists for want of which so much effort is wasted and progress is so slow.

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EXPERIMENTS IN THE CROSSING OF LOCAL RACES OF LEPIDOPTERA

[*The Entomologist's Record*, 1898]

Among the various objects of zoological interest placed in the zoological laboratory were exhibits by Mr Bateson, illustrating experiments in the crossing of local varieties. Two species were especially interesting, viz. *Pararge egeria* and *Pieris napi*. In the case of *P. egeria*, the forms of the species occurring in western Europe were well illustrated by a large blackboard, on which was sketched a map of western Europe, and actual specimens were pinned on the board at approximately their places of capture on the map. This arrangement exhibits at once to the eye the distribution of *P. egeria* and var. *egeriades*, and did so completely for the purpose of the exhibit, though for faunistic purposes a map taking in a larger area would no doubt be necessary. (1) The southern form (*egeria*) was shown to inhabit Spain, western France, south of the Loire, and the lower Rhone Valley, the actual localities being Gibraltar, Granada, Jaen, Biarritz, Landes, Vienne, Poitiers, Avignon, Tarascon. (2) The middle form (var. *intermedia*) occupied a zone round this, viz. the lower Loire Valley, Brittany, Savoy and the Riviera, the localities illustrated being Avranches, Cancele, Balleroy, Gavrinis, Chambéry, Nice. (3) The northern and Alpine form (*egeriades*) occupied England, Paris, Doubs, examples being shown from Paris, Caen, Besançon, England. It was interesting to note the influence of the proximity of the Alps in bringing the middle form to the Riviera, where the southern form would, the Alps apart, have been a more likely form. Those from Nice were almost more *egeriades* than *egeria*, when compared with the representatives of these forms on the map, and must be within the influences of crossing with Alpine races. The northern form, in one of its types, is no doubt well known to most of our readers; the southern one varies somewhat from different localities. It has comparatively little black marking, and the fulvous is so bright and red that the superficial aspect of the specimens to a British eye is much more that of *P. megæra* ♂ than *P. egeria*. Mr Bateson shows a number of broods bred from crossing of the extreme forms. There

are no doubt many points of interest to be elucidated from these when fully studied. We noticed, for instance, in one or two broods a tendency to increase the *Vanessa*-like angle to the fore-wing, of which *P. egeria* usually shows somewhat more indication than the mass of Satyrids. The point that Mr Bateson emphasises is that there is practically no indication of discontinuous variation in the various broods. The specimens may broadly be described as all falling within the limits of the middle form, none tending to be either of the southern or northern type, still less no tendency of any brood to divide into two groups.

The other portion of Mr Bateson's butterflies is more interesting. These consist of numbers of broods showing the results of crossing *Pieris napi* of the Italian form with *Pieris* var. *bryoniæ*. It is generally believed, and is probably true, that *bryoniæ* is a single-brooded form. Mr Bateson, however, shows a summer brood of *bryoniæ*, artificially reared by him in England. These are like no forms of *P. napi* that we remember to have seen, certainly, at least, not in quantity, as a race. The most curious feature they have is a strong tendency to a dark border, on the pattern of *Colias*. This same tendency crops up in some of the crossed broods. The crosses, both between the two forms and between either form and the crossed progeny, appear to be quite fertile. Besides the number of unusual forms of *P. napi* which they present, it is remarkable that some broods appear to be fairly intermediate between the parent forms, whilst in others the specimens are fairly spread throughout the interval between them, and in one or two there is marked *discontinuity*, one portion of the brood favouring *P. napi*, the other, var. *bryoniæ*, but with few intermediate specimens. These various results in crosses of the same forms are of extreme interest, and we shall await with much expectation the full details of the results when Mr Bateson has secured and analysed the material he is now accumulating.

We had the pleasure of seeing Mr Bateson's garden in which these experiments are carried out, and admired the simplicity and completeness of the arrangement for these experiments. He finds no difficulty in getting the butterflies to pair and oviposit. The apparatus consists of a box placed in the garden, open to the weather, and covered with gauze. The box is about $30'' \times 18''$, and contains a supply of flowers in a glass and of the food-plant growing in a pot. Some shade is provided by a partial covering of canvas thrown loosely over. Mr Bateson has long ranges of these boxes and of pots of the

food-plants to which the insects may be removed and on which they are sleeved after oviposition has been completed.

He exhibited also the tegumina of the ♂s of *Anthrocera loniceræ* and *A. filipendulæ*, and of the hybrids raised by Mr W. H. B. Fletcher. These showed a great difference between the two species, whilst in the hybrid the form is intermediate.

THE INHERITANCE OF VARIATION IN THE COROLLA OF *VERONICA BUXBAUMII*

[*Proceedings of the Cambridge Philosophical Society*, x, 1900]

(With Plate VII)

In a former paper[1] an account was given of certain variations in the form of the corolla of *Veronica Buxbaumii*. It was shown that abnormal flowers were of common occurrence and that certain symmetrical forms of variation were especially frequent. Flowers taken at random on heavy clay arable land near Cambridge showed about 6 per cent. of flowers with three petals, and about 1 per cent. of flowers with two petals. Occasional 5-petalled flowers having either two posterior petals or two anterior petals were also seen. Various irregular forms were found, but these were of comparatively rare occurrence.

Further observation showed that in garden ground the 5-petalled forms were by no means rare, that with two posterior petals being especially common. As indicated above, there appear to be considerable differences between the variations found in different localities. These differences may possibly be connected with the nature of the soil, but this aspect of the matter has not been further examined.

It was pointed out that though the 2-posterior-petalled form may reasonably be regarded as of the nature of reversion, the other forms cannot be so regarded, though they are no less perfectly formed, and are much more common than those imperfectly formed flowers which may be described as intermediate between the type and the perfect variations.

The experiments described in this paper were undertaken to test whether there is any difference between offspring raised from abnormal flowers, and the offspring of normal flowers borne by the same plant. The possibility that there may be a difference in inheritance in such cases is referred to by some writers, especially by practical horticulturists, and the theoretical importance of the question is of course considerable. Apart however from a few cases (like that of the peach and the nectarine) in which seed from a sporting branch has

[1] *On Variations in the Floral Symmetry of certain Plants having Irregular Corollas*, by W. Bateson and A. Bateson. *Journ. Linn. Soc.* Bot. xxviii, 1891, p. 386 [p. 126, *supra*].

been observed to transmit the peculiarities of the branch, it does not appear that much evidence bearing on the question exists.

It should be noticed that the analogy between the present case and that of the sporting branches is not in all respects precise, and in particular that the variations we are about to describe are essentially meristic. In the absence of evidence there does not appear to be any probability that because in a flower one or more whorls show an abnormal division, the reproductive elements carried by the flower should produce individuals more abnormal than those proceeding from normally divided flowers on the same plant.

In the following experiments, which were entirely carried out by Miss Pertz, the evidence, though scanty, goes on the whole to show that there is, at all events in the case investigated, no well-marked difference between the offspring of normal and abnormal flowers.

Amongst plants raised from seed taken out of the same self-fertilised capsule great diversity of variability was constantly manifested, but there was no indication that families of plants raised from capsules formed by self-fertilisation of abnormal flowers in general showed either greater variability or greater percentage of any one abnormal form than families similarly raised from normal flowers on the same plant. On the contrary the evidence tends to show that the self-fertilised offspring of normal and abnormal flowers on the whole conform to an equal degree with the general characteristics of the parent plant, or more strictly of the strain or race to which the parent belonged. In the course of the work a few collateral points of some interest were made out.

The forms of corolla most frequently occurring are as follows:

1. *Normal* flowers (Fig. 1). These are the ordinary flowers characteristic of the genus. The corolla consists of four petals. Of these one is posterior, one anterior, and two lateral. The posterior petal is wide and of a deep blue colour. Opposite to it is the narrower anterior petal, of a pale bluish-white colour. The lateral petals are of about the same size as the posterior, but in intensity of colour they are intermediate between the posterior and anterior petals.

Generally speaking these normal flowers form 80–90 per cent. of the whole but, as may be seen in the Tables, they may on particular plants form a much higher or a much lower percentage than this.

2. *Corolla with two anterior petals* (Fig. 3). These corollas possess one posterior and two lateral petals like the normal, but differ in

having the anterior petal represented by two petals. These two petals are like the normal anterior petal in form and colour. Like the normal also they are small petals but not unfrequently they are somewhat unequal in size.

3. *Corolla with two posterior petals* (Fig. 2). Flowers like the normal except that the posterior petal is represented by two petals, each more than half the size of the normal one.

As it may reasonably be supposed that the one posterior petal of *Veronica* represents the two posterior petals of 5-petalled Scrophulariaceæ, these corollas with two posterior petals can very plausibly be considered reversions. At all events, of the various forms seen this is the one which can with most reason be supposed to represent a form actually passed through in the evolution of the species. Hence it is of interest to note that this is the only one of the common variations which is connected with the normal by any considerable number of intermediate forms. In these the posterior petal is more or less cleft into two (Fig. 19). In the lower forms of the variation the place of division is only indicated by a notch. Such a variation is of course an example of the phenomenon of division in a plane about which there is bilateral symmetry, a phenomenon constantly occurring in animals and plants[1]. By reference to the Tables it will be seen that these intermediates occasionally form a fairly high proportion of the abnormal flowers, though even in these cases the complete form of the variation is as a rule the more frequent on the same plant.

4. *Corolla with six petals*, two being posterior and two anterior (Fig. 5). These flowers present the peculiarities of both the 2nd and 3rd forms of variation mentioned above. The anterior two petals here also are not infrequently unequal in size, and the division between the two posterior petals may be incomplete (see No. 3).

5. *Corolla with three petals* (Fig. 4). In this form the posterior petal is normal. There is no anterior petal, the corolla being completed by two large lateral petals. The appearance suggests that the material usually composing the two laterals and the anterior has been divided by one median division into two. Not rarely there is at the anterior edges of these two petals a band of lighter colour, showing that the colour still follows the normal distribution of the 4-petalled flower. This is however by no means always the case.

[1] See *Materials for the Study of Variation*, 1894, p. 448.

6. *Corolla with two petals* (Fig. 20). The whole corolla is here formed of two petals, placed as anterior and posterior respectively. They are of about equal size.

7. *Corolla with four petals set obliquely* (Fig. 7). In this form the petals stand as two anteriors and two posteriors, forming an oblique instead of an upright cross. The morphology of this flower is not quite clear, but there seems little doubt that it should be regarded as a corolla in which the posterior petal has been divided as in Fig. 2, while the anterior and lateral elements have developed in the same way as those shown in Fig. 4.

Occasional forms. Besides the forms enumerated above, of which all are found in some quantity, there are various other forms of only occasional occurrence. Of these some are symmetrical, *e.g.* corollas having three posterior petals making six in all (Fig. 11); corollas having 7 or 8 petals, viz. 3 or 4 anterior, 3 or 4 posterior (Fig. 10). There are besides these asymmetrical forms of variation, in which for example one of the lateral petals is smaller than the other, and so forth, but none of these are found in any quantity.

Small flowers. In the previous paper mention was made of a peculiar form of flower having its parts, especially the corolla, of very small size (Fig. 18). These flowers were of occasional occurrence only.

Calyx. The calyx is also liable to numerical variations, but no record of these was kept. There are frequently variations of the calyx in correlation with those of the corolla, but not rarely the one whorl may be abnormal while the other is normal.

Stamens and *Pistil.* Variations in these parts were extremely rare.

Method. The plants selected in each year for self-fertilisation were potted and completely isolated, usually by means of a bell-jar over water, or a fine muslin net. Before covering, the flowers then open were all cut off, and the artificial self-fertilisation was not begun until the following day. The self-fertilised flowers were marked with coloured threads and the cover left on the plant until the corollas of these flowers had fallen off. The cover was then removed and the capsules ripened in the open.

The seeds were sown either in the autumn or in the early spring.

The seeds from each selected capsule were sown in separate pots, and afterwards pricked out in an open piece of ground in the Botanic Garden.

The flowers, which open in the morning, were counted during the morning hours on as many days as possible during the flowering season.

Except during the first weeks of 1892 each flower was picked as it was noted, thus all danger of repetition was avoided.

By these successive countings the relative numbers of each kind of flower borne by each plant during its flowering period were approximately obtained. In a good many cases days were missed, and in 1894 and 1895 the plants had not altogether finished flowering when the counting stopped. We have not attempted to make any correction for this, but there is no reason to suppose that the results are thereby materially affected.

In the Tables the number of each kind of flower is given as a percentage of the total number of flowers borne by the plant. This total is given in the right-hand column of each Table. In the bottom line of each Table is given the average percentage of each kind of flower borne by the whole family sprung from one capsule. This average is calculated on the grand total of flowers borne by the whole family.

It is noticeable that while there is very great diversity among the offspring of the same self-fertilised capsule, yet the *average* degree of abnormality in the family generally remains fairly constant for the descendants of each original plant.

The extraordinary irregularity in the percentages amongst these offspring of self-fertilisation is not a little remarkable. It might perhaps have been expected that as the result of successive self-fertilisation some diminution in variability would occur. So far as our figures go, there is no indication of such a result.

An attempt was made to discover whether the abnormal flowers were produced with any greater frequency at one part of the flowering period than at another. Decided evidence was found that this is so. Though there are not a few exceptions, the countings show in a large majority of cases that the chief output of abnormal flowers takes place in the earlier part of the flowering season and especially just before the greatest output of flowers, after which time the percentage of abnormality declines. It was not thought worth while to print the detailed records on which this statement is based.

The plants studied, 135 in all, were severally descended from three original plants, and the descendants of each of these three are referred to as Race I, Race II, and Race III respectively.

Race I. The original plant from which Race I descended was

growing wild in a plot of waste garden-land near Cambridge. On it five flowers were chosen, being respectively A, normal; B, two anterior petals; C, D and E, each having two posterior petals. As to the fertilisation of these flowers nothing was known.

From these flowers the first generation was raised and the succeeding generations were produced by self-fertilisation, the detailed pedigrees being given in the Tables.

The most noticeable characteristic of this Race is the high average percentage of flowers with two posterior petals. It will be seen that this percentage is exceedingly variable. In the first sowing there are some high percentages of 3-petalled flowers on certain plants, especially of the families C and D. It is of course possible that these were fertilised by pollen from other plants, but in the family A_5A there are also a few such plants. In subsequent generations of the Race the decline in 3-petalled flowers is rather striking and we have no indication of the reason for this.

If the 1st generation stood alone it would seem that the percentage of abnormality was greatest in the offspring of abnormal flowers. Subsequent generations nevertheless are quite at variance with such a result.

Race II. The seed was taken from the capsule of a flower of unknown form on a plant in the same locality as the parent of Race I. The Race is remarkable for a high percentage both of 2-posterior-petalled flowers and also 3-petalled flowers. It will be noticed that in the 2nd generation the percentage of 2-posterior-petalled flowers happens to be highest in a family the offspring of a normal flower.

Race III. In the summer of 1893 a plant was observed growing wild in the Botanic Garden which bore an unusual number of 3-petalled flowers. A capsule which had not been in any way protected from cross-fertilisation was gathered, and the seeds produced four plants. The contrast between these and Races I and II is very marked. The form with two posterior petals is here extraordinarily scarce, while the flowers with three petals are in the high proportion of four per cent. The next generation of the Race maintained the same characteristics. From this Race alone it might be inferred that an abundance of the 3-petalled form is not compatible with a considerable number of flowers having two posterior petals, but several plants in the other Races show that this is not the case (*e.g.* Race II, A_1 and A_1A_2).

TABLES

In the following Tables:

N	stands for	normal
2*a*	,,	2 anterior petals
2*pp*	,,	2 posterior petals
6	,,	6 petals
3	,,	3 ,,
2	,,	2 ,,
$4\frac{2}{2}$	,,	the form numbered 7 in the text
Int.	,,	intermediates between normal and 2*pp*
Misc.	,,	miscellaneous forms not included in the above categories.

The number of flowers of each category given in percentages of total flowers printed in right-hand column.

In the case of some of the scarcer forms the percentage is given to the second place of decimals. Most are only taken to the first place.

Race I

1892. *First Generation.* On one plant 5 capsules were taken, viz.:

	A	B	C	D	E
	normal flower	2 ant. pet. fl.	2 post. pet. fl.	2 post. pet. fl.	2 post. pet. fl.
From these grew	5 plants	3 plants	4 plants	3 plants	1 plant

Result.

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
A 1	91·5	2·3	4·2	·6	·5	—	—	·7	·2	1398
2	96·8	1·1	1·6	·2	—	—	—	·2	·1	1218
3	82·2	1·8	11·6	1	1·3	—	·4	1·2	·3	1050
4	88·4	2·9	4·9	·6	1·7	·02	1	1	·2	4787
5	69·4	3	17·9	4·4	2·7	·3	1·1	·4	·9	666
Averages	87·9	2·4	6·1	·8	1·3	·03	·1	·7	·3	9119

(Seed taken from A_1, A_4, A_5.)

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
B 1	70·4	1·9	19	2·4	3·3	·2	·7	1·4	·1	3236
2	75·7	3·4	13·9	2·1	2·3	·1	·6	1·5	·3	2789
3	83·6	1·5	8·3	·9	3·6	·1	·5	1·2	·1	4781
Averages	77·7	2·1	13·1	1·7	3·1	·1	·6	1·3	·2	10806

(No seed taken.)

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
C 1	72·2	2·1	20	2·1	1·6	·1	·4	·5	·2	2869
2	74·1	7·4	14·9	1·9	·8	—	·4	·4	·5	2151
3	81·9	6	8·1	2·1	—	·1	·1	·2	·5	2106
4	80·9	4·2	9·9	1·3	2·1	—	·1	·8	—	2740
Averages	77·1	4·7	13·5	1·9	1·6	·1	·3	·5	·3	9866

(No seed taken.)

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
D 1	69·4	1·7	21·9	2·5	2·7	·2	—	1·4	·4	474
2	76·9	2·3	16·7	1·5	1·7	—	·04	·2	·3	2306
3	69·4	2·7	17·2	2·4	5·2	·4	·6	1·3	·5	1044
Averages	73·9	2·3	17·5	1·9	2·8	·2	·2	·9	·4	3824

(No seed taken.)

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
E	80·8	5·1	9·1	2·1	1·2	—	·7	·2	·6	1142

1893. *Second Generation.* On A_1 one capsule was taken, viz.:

6 pet. flower, A_1 A

From this grew 6 plants

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
A_1A 1	81·2	3·6	10·1	—	·5	—	·5	2·8	1·4	218
2	87·3	—	7·5	·2	1·3	·2	—	3·3	·2	455
3	86·6	7·3	3·7	—	—	—	—	2·4	—	82
4	65·9	2·3	20·4	—	—	—	—	10·2	1·1	88
5	100	—	—	—	—	—	—	—	—	8
6	91·2	—	8·8	—	—	—	—	—	—	34
Averages	83·9	1·8	9	·1	·8	·1	·1	3·6	·6	885

(Seed taken from A_1 A_2.)

On A_4 one capsule was taken, viz.:

6 pet. flower, A_4 A

From this grew 6 plants

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
A_4A 1	68·5	10·5	14·5	2·6	—	1·3	—	2·6	—	76
2	51·3	15·4	25·6	2·6	2·6	—	—	2·6	—	39
3	71·2	1·5	25·8	—	1·5	—	—	—	—	66
4	58·1	3·7	29·9	3·7	1·6	—	—	1·9	1·1	377
5	65·1	5·2	21·9	3·2	·9	—	—	3·5	·9	324
6	83·6	8·9	5·5	—	—	2·5	—	—	—	166
Averages	64·9	5·7	22·4	2·6	1·1	·6	1·1	2·1	·7	1048

(No seed taken.)

On A_5 one capsule was taken, viz.:

3 pet. flower, A_5A

From this grew 17 plants

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
A_5A 1	84·4	2·6	7	·9	·9	—	·3	3·3	—	340
2	83·1	4·2	8·7	·4	·6	—	—	2·8	·2	528
3	80·9	2·1	10·6	—	4·3	—	—	2·1	—	47
4	87·5	2	4·2	·5	3·7	—	·2	1·8	·2	598
5	81·2	9·4	1·6	·8	1·1	—	—	3·2	—	373
6	84·9	5·3	3·4	·6	1·8	—	—	3·5	—	318
7	89·7	4·3	1	·5	3·8	—	·5	—	—	185
8	89·1	3·3	3·6	·6	—	—	·3	2·1	·6	329
9	81·4	7·8	3·9	—	·9	—	—	4·9	·9	102
10	97·4	—	—	—	—	—	—	2·5	—	39
11	90·9	5·3	3·4	—	—	—	—	·4	—	263
12	85·7	3·1	7·7	·7	1·7	—	—	·7	·3	287
13	92·4	2·5	1·3	—	2·5	·6	—	·6	—	157
14	87·4	5·8	2	·7	1	—	·7	2·4	—	294
15	92·6	2·1	·7	—	1·8	—	—	2·5	·3	283
16	77·7	1·9	15·5	1·9	·9	—	—	1·9	—	103
17	88·7	4·4	2·9	—	2·9	—	—	·5	—	211
Averages	86·6	4·1	4·4	·5	1·6	·02	·1	2·1	·3	4457

(No seed taken.)

On E two capsules were taken, viz.:

normal fl., EA — 2 ant. pet. fl., EB

From these grew 7 plants — 7 plants

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
EA 1	77	13·3	3·9	1·5	·6	—	—	3	·6	330
2	74·3	13·3	6·8	1·6	·5	—	—	2·7	·8	443
3	69·8	15·2	5·2	3·7	2·1	—	—	3·7	—	328
4	73	14·8	6·6	2·9	·3	—	—	1·6	—	379
5	64·1	9·4	9·4	1·9	—	1·9	1·9	11·3	—	53
6	60·8	12·7	15·4	5·6	1·6	—	—	3·9	—	306
7	67·5	13·5	9·7	4	1·6	—	1·6	2·4	—	126
Averages	70·9	13·7	7·6	2·9	1	·1	·1	3·1	·3	1965

(No seed taken.)

	N	2*a*	2*pp*	6	3	2	$4\frac{3}{5}$	Int.	Misc.	Totals
EB 1	87	3·2	7·3	—	·8	·8	—	·8	—	247
2	72·5	9·2	15	·8	—	—	—	2·5	—	120
3	93·3	3·3	—	—	—	—	—	3·3	—	30
4	65·2	11·9	13·4	1·8	2·2	·4	—	3·6	1·4	276
5	67·2	11·9	12·3	3·6	·6	—	·2	3·6	·8	530
6	81·6	7·9	2·6	2·6	—	—	—	5·3	—	38
7	72·3	17·9	5·8	—	·3	·3	—	2·5	1·1	364
Averages	72·3	11·5	9·9	1·6	·7	·2	·1	2·9	·7	1605

(No seed taken.)

1894. *Third Generation.* On A_1A_2 three capsules were taken, viz.:

From these grew	normal fl., A_1A_2A | 9 plants	2 post. pet. fl., A_1A_2B | 7 plants	3 pet. fl., A_1A_2C | 6 plants

	N	2*a*	2*pp*	6	3	2	$4\frac{3}{5}$	Int.	Misc.	Totals
A_1A_2A 1	93·7	·7	4·2	·1	·4	—	—	·9	—	1709
2	71·3	—	26·9	·3	·7	·1	·1	·4	—	897
3	91·2	·6	6·7	·2	·3	—	·1	·7	·1	1564
4	97·4	·4	2·1	—	—	—	—	—	—	1359
5	63·1	·2	34·5	·5	·5	—	·1	1·1	—	1288
6	95·3	·9	3·5	—	·2	—	—	—	—	846
7	92·9	·7	5·7	—	·4	—	—	·3	—	1163
8	85·7	1	10·2	·2	·2	—	—	1·8	—	1201
9	93·3	1·1	4·5	—	1·1	—	—	—	—	449
Averages	87·5	·6	10·8	·2	·4	·01	·02	·6	—	10476

(Seed taken from $A_1A_2A_3$ and $A_1A_2A_5$.)

	N	2*a*	2*pp*	6	3	2	$4\frac{3}{5}$	Int.	Misc.	Totals
A_1A_2B 1	98·5	—	·2	1·3	—	—	—	—	—	1152
2	94·7	·7	3·8	—	·2	—	—	·5	—	1406
3	78·9	·7	17·6	·7	—	—	—	2·1	—	142
4	81·8	4·1	12·4	—	·3	—	—	1·2	—	314
5	93·3	—	4·2	—	·4	—	—	2·1	—	239
6	67·9	—	30·4	—	—	—	—	1·7	—	181
7	84·5	2·1	11·7	—	—	—	—	1·6	—	187
Averages	92·2	·8	6·1	·02	·1	—	—	·6	—	3621

(Seed taken from $A_1A_2B_4$.)

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
A_1A_2C 1	96·7	·3	2·7	·05	·05	—	—	·2	—	1839
2	86·8	·8	11·1	·7	·2	—	—	·5	—	621
3	96·4	·8	2·3	—	·1	·04	—	·4	·04	2242
4	97·4	·2	1·7	·2	·3	—	—	·2	—	618
5	95·4	·5	3·3	·1	·4	—	—	·3	—	2401
6	97·6	·6	1·2	·1	·3	—	—	·2	—	1265
Averages	95·8	·5	3·1	·1	·2	·01	—	·31	—	8986

(No seed taken.)

1895. *Fourth Generation.* On $A_1A_2A_3$ two capsules were taken, viz.:

normal fl., $A_1A_2A_3A$ — 2 post. pet. fl., $A_1A_2A_3B$

From these grew — 7 plants — 4 plants

		N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
$A_1A_2A_3A$	1	92·6	1·9	5	·2	·5	—	—	·6	—	967
	2	83·8	·9	12·8	·9	·2	·2	—	1·1	—	618
	3	84·8	2·1	10·6	·4	·3	—	—	·9	—	778
	4	84·9	1·3	10·3	·4	·2	—	—	2·8	—	464
	5	80·7	7·2	9	1·7	·7	—	—	·7	—	290
	6	80·3	5	12·9	—	·7	—	—	1·1	—	279
	7	87·4	2·5	7·3	·8	·3	—	·3	1·5	—	398
Averages		86	2·4	9·3	·6	·4	·02	·02	1·1	—	3794

(No seed taken.)

		N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
$A_1A_2A_3B$	1	90·7	2·6	5·6	·1	·2	—	—	·7	—	836
	2	94·1	·9	3·9	—	·2	—	—	·8	—	883
	3	85·3	2	12·4	—	·1	—	—	·1	—	744
	4	80·6	2·2	15·2	·4	—	—	—	1·4	·1	696
Averages		88·2	1·9	8·9	·1	·2	—	—	·8	—	3159

(No seed taken.)

On $A_1A_2A_5$ two capsules were taken, viz.:

normal fl., $A_1A_2A_5A$ — 2 post. pet. fl., $A_1A_2A_5B$

From these grew — 1 plant — 6 plants

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Total
$A_1A_2A_5A$	66·2	7·2	20·9	2·6	·9	—	—	1·8	—	607

(No seed taken.)

		N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
$A_1A_2A_5B$	1	92·4	1	4·7	·2	—	—	—	1·5	—	386
	2	88·3	1·5	8·5	·2	·3	—	—	1·2	—	616
	3	85·4	1·3	10·5	1·3	·2	—	—	1·7	—	604
	4	82·9	1·3	13·5	·4	·2	·2	—	1·5	—	533
	5	84·1	1·6	11·5	·2	·5	·2	—	2·1	—	634
	6	91·1	1·3	6	—	·4	—	—	1·1	—	531
Averages		87·1	1·4	9·3	·4	·3	·02	—	1·5	—	3304

(No seed taken.)

On $A_1A_2B_4$ two capsules were taken, viz.:

normal fl., $A_1A_2B_4A$ — 2 post. pet. fl., $A_1A_2B_4B$

From these grew 4 plants — 4 plants

		N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
$A_1A_2B_4A$	1	93·5	·7	4·3	·4	·3	—	—	·8	·1	783
	2	92·4	1·9	3·9	·3	·7	—	—	·5	—	554
	3	81	1·2	15·4	·7	·3	—	—	1·2	—	589
	4	89·6	1·7	7·4	·2	·2	—	—	·9	—	527
Averages		89·4	1·3	7·5	·4	·4	—	—	·8	—	2453

(No seed taken.)

		N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
$A_1A_2B_4B$	1	57·5	·7	39·7	·2	·3	—	—	1·5	—	546
	2	79·4	1·9	16·9	—	—	—	—	1·9	—	373
	3	86	1·9	9·6	·2	·2	—	—	2·1	—	428
	4	90·9	1·1	6·9	—	·1	—	—	·9	—	539
Averages		77·8	1·3	18·9	·1	·2	—	—	1·5	—	1886

(No seed taken.)

Race II

1892. *First Generation.* On one plant one capsule was taken, viz.:

flower, form unknown, A

From this grew 2 plants

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
A 1	51·6	—	40·3	4·8	3·2	—	—	—	—	124
2	67	·7	29·1	1·1	1·8	—	·4	—	—	285
Averages	62·3	·5	32·5	2·2	2·2	—	·2	—	—	409

(Seed taken from A_1.)

1893. *Second Generation.* On A_1 two capsules were taken, viz.:

normal fl., A_1A — 2 post. pet. fl., A_1B

From these grew — 5 plants — 2 plants

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
A_1A 1	57·7	1·7	39·1	—	—	—	—	1·5	—	402
2	69	·9	19·7	·4	4·4	—	·4	4·9	—	223
3	86·7	—	6·6	—	6	—	—	·6	—	165
4	90	—	5	—	—	—	—	5	—	20
5	78·7	6·1	9·6	—	3·1	1·1	—	1·1	—	94
Averages	68·6	1·6	24·5	·1	2·5	·1	·1	2·2	—	904

(No seed taken.)

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
A_1B 1	76·5	·4	18·9	·4	3·3	—	—	·4	—	238
2	73	·8	20	—	3·8	—	—	2·1	—	234
Averages	74·9	·6	19·3	·2	3·5	—	—	1·2	—	472

(No seed taken.)

Race III

1894. *First Generation.* On one plant one capsule was taken, viz.:

flower, form unknown, A

From this grew — 4 plants

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
A 1	95·8	—	·1	—	3·5	·3	—	·2	—	2592
2	95·1	—	·04	—	4·6	·2	—	·04	—	2074
3	94·7	·1	·1	—	4·5	·5	—	—	—	1929
4	93·8	—	—	—	5·3	·7	—	·2	—	1808
Averages	95·2	·03	·1	—	4·4	·4	—	·11	—	8403

(Seed taken from A_4.)

1895. *Second Generation.* On A_4 two capsules were taken, viz.:

normal flower, A_4A — 3 pet. flower, A_4B

From these grew — 6 plants — 9 plants

	N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
A_4A 1	92·9	·4	—	—	5·4	1·1	—	·2	—	448
2	92·9	·8	—	·2	5·6	·2	—	·5	—	611
3	89·6	1·3	·2	—	6	1·5	—	1·3	—	461
4	93·5	1·3	—	—	3·9	·5	—	·8	—	618
5	92·1	1·8	—	—	4·9	1·1	—	·1	—	717
6	94·1	·7	·1	—	4·4	·2	—	·4	—	804
Averages	92·6	1·1	·05	·02	4·9	·7	—	·54	—	3659

(No seed taken.)

		N	2*a*	2*pp*	6	3	2	$4\frac{2}{2}$	Int.	Misc.	Totals
A_4B	1	94·6	·5	·2	—	4·4	·1	—	·1	—	1058
	2	90·9	·5	·1	—	7·3	1·1	—	·1	—	1460
	3	92·2	—	·1	—	6·8	1·7	—	·1	—	825
	4	94	2·6	·4	—	2·2	·1	—	·7	—	737
	5	91·9	·6	·2	—	5·9	·9	—	·3	—	1172
	6	92·3	·6	·2	—	5·2	1·1	—	·5	—	854
	7	94·5	·4	·3	—	3·9	·8	—	·1	—	1161
	8	91·1	·7	—	—	6·8	1·4	—	—	—	839
	9	90·7	·7	·3	—	7·6	·8	—	—	—	899
Averages		92·5	·7	·2	—	5·7	·8	—	·2	—	9005

(No seed taken.)

Explanation of Plate VII

Fig. 1. Normal flower.

Fig. 2. Two posterior petals.

Fig. 3. Two anterior petals.

Fig. 4. Three petals.

Fig. 5. Six-petalled form having two posterior and two anterior petals.

Fig. 6. Rare form with three petals.

Fig. 7. Four petals set obliquely.

Fig. 8. Corolla with division of posterior petal indicated by a *fold* seen from behind.

Fig. 9. Three anterior petals.

Fig. 10. Two posterior petals combined with three anterior petals.

Fig. 11. Three posterior petals.

Fig. 12. Lateral petal divided.

Figs. 13 and 14. Irregular forms.

Fig. 15. Corolla like Fig. 7, but having imperfect division between posterior petals.

Fig. 16. Irregular form.

Fig. 17. A very peculiar corolla. All the petals are unusually narrow and the posterior is divided, the two halves being separated by a space.

Fig. 18. A "small flower" (see p. 377).

Fig. 19. *a*, *b*, *c*, various forms of notching or imperfect division of posterior petal. *d*, appearance of trifid division in posterior petal.

Fig. 20. Two-petalled corolla.

[Plate VII has been reproduced by process from the lithographic original. Ed.]


1


2


3


4


5


6


7


8


9


10


11


12


20


13


14


15


16


17


a


b d


c


18

A CASE OF HOMŒOSIS IN A CRUSTACEAN OF THE GENUS *ASELLUS*

[*Proceedings of the Zoological Society*, 1900]

THE subject of this note is a male specimen of *Asellus aquaticus* (an Isopod Crustacean) in which the left antennule is represented by a mandible.

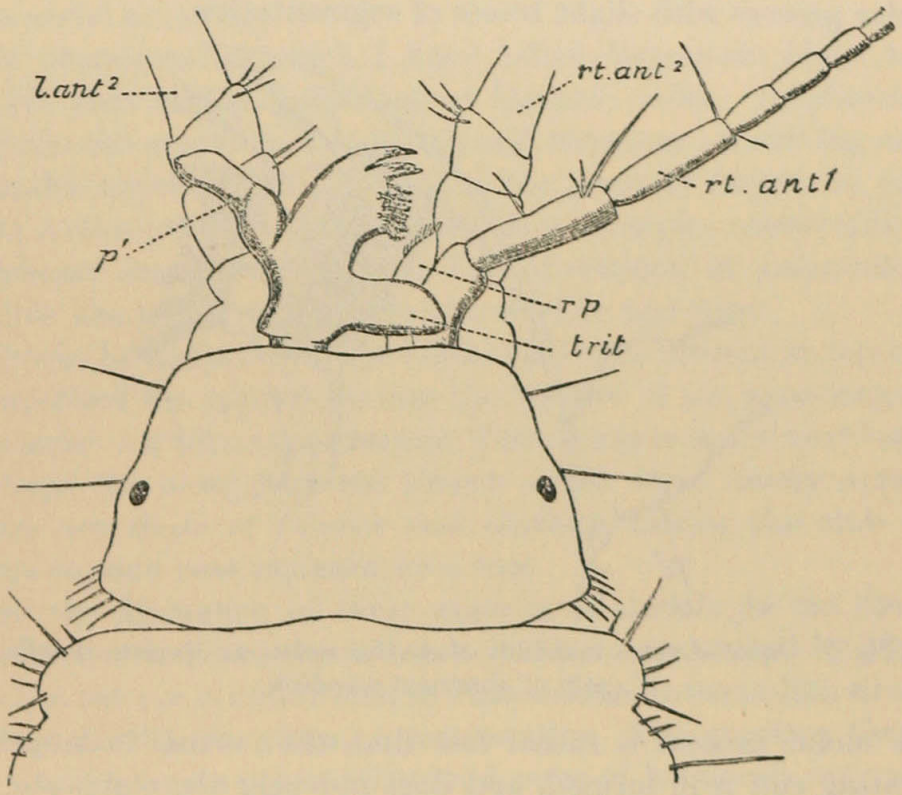


Fig. 1. Head of *Asellus aquaticus*, seen from dorsal side—*rt. ant.*¹, right antennule; *rt. ant.*², *l. ant.*², right and left antennæ; *rp*, palp of normal right mandible projecting from below; *p'*, palp of the abnormal mandible; *trit*, triturating process.

The specimen was noticed when alive by Mr. J. J. Lister among a number of *Aselli* taken from a large aquarium in the Cambridge Zoological Laboratory for examination by the students.

As the figure shows (Fig. 1), the abnormal structure stands exactly as the left antennule should. Both antennæ and the right antennule are normal, as also are the mandibles, the other mouth-parts, and the rest of the body and its appendages, so far as they could be observed. The animal was of good size.

The abnormal appendage (Fig. 2, p. 390) is a fairly well-formed mandible. The blade is complete, having two toothed processes and eleven plumose setæ. The latter are not quite regularly placed. The presence of *two* toothed processes proves that the appendage is a true

left appendage, for the right mandible in *Asellus aquaticus* has only one toothed process, which bites between the two toothed processes of the left mandible[1].

The teeth on these processes are more numerous and less regular than in a normal mandible.

The palp is misshapen and rudimentary. It consists merely of an irregular process with slight traces of segmentation.

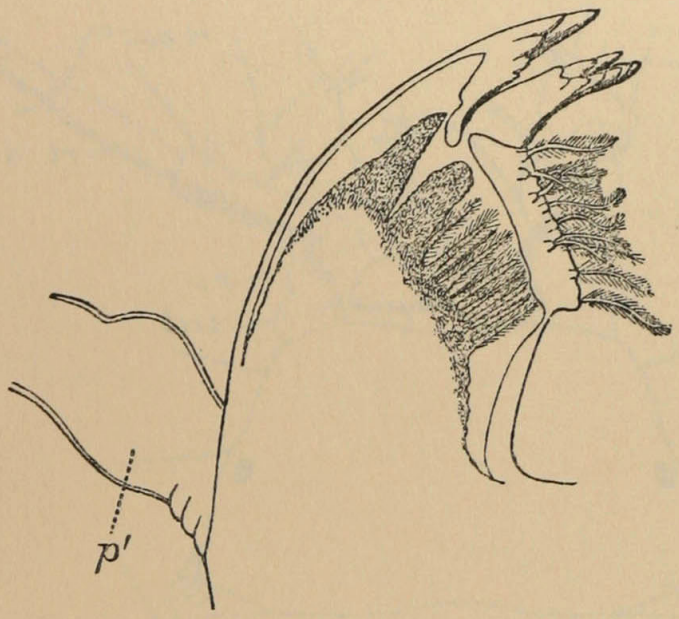


Fig. 2. Apex of extra mandible of *Asellus aquaticus*, to show details. *p'*, palp of abnormal mandible.

The molar process is rather less than the normal in length. Its triturating end is ill-formed, and does not bear the elaborate structures found in the same place in the normal mandible, the apex being simply covered with a thick plate of chitin.

The mandible was in life carried flat to the body, as shown in the drawing, but I have not succeeded in determining which morphological surface was upwards. It is not evident which this should be, but presumably it is the face, which in the normal mandible is next the mouth. I regret that I could find no feature sufficiently differentiating the two surfaces; but from the fact that, as shown in the figure, the diminishing series of teeth are on the exposed surface, it seems likely that the presumption referred to is correct. In a normal mandible this series is much less clearly defined.

The animal was approaching a moult, and the newly-formed skin, which could be seen through, showed that at the next ecdysis the appendage would not be noticeably changed.

[1] Sars, G. O., *Crustacés d'Eau douce de Norvège*, p. 97, Pl. VIII, fig. 26.

In the details of the toothing and in the number of the plumose setæ (11 instead of 13), the animal departs slightly from Sars's type; but on examining other specimens I find that these characters vary a good deal, as might be expected.

Elsewhere[1] I have discussed the significance of cases of this sort, in which an organ takes on the likeness of another organ with which it is in serial homology.

This phenomenon, which I have called *Homœosis*, plays a considerable part in the variations of Meristic series. In plants such variations are common, but in animals instances so striking as that now under consideration are among the greatest rarities in nature. Among Arthropods probably not a dozen examples comparable with the present one are on record. The conversion of antennule into mandible has not hitherto been observed in any form.

It should be noticed that the homœosis in the present instance does not transform the appendage into the likeness of the appendage next to it in series, for this is the antenna. The change is to the next but one.

Perhaps the cases hitherto known which most nearly approach this one are those of *Cimbex* and *Bombus*, having the club of an antenna in each case replaced by a foot.

Since the discussion of these cases in *Materials for the Study of Variation* was written, the new fact has been discovered by Herbst[2] that when the eye is amputated in *Palæmon* an antenna-like structure may be formed in its place on regeneration. The question therefore arises whether some other Arthropod cases of homœosis may not be similarly connected with regeneration. On this point there is little positive evidence. It may be noted, however, that Przibram[3], who made some experiments on the subject, found that in *Asellus* both pairs of antennæ were regenerated as antennæ[4]. The results of such experiments, however, are clearly very irregular. The regenerated part in Herbst's experiments was not always similar, and Przibram, on repeating Herbst's experiments, obtained only negative results. Here the matter at present rests.

[1] Especially *Materials for the Study of Variation*, Chap. v, where an account of previously recorded cases is given. To these should be added a case of an *Astacus* having a somewhat antennuliform structure with two jointed filaments replacing one of the eyes: Hofer, B., *Verh. d. deutsch. zool. Ges.* IV, 1894, p. 82, fig.

[2] *Arch. f. Entwickelungsmech.* II, 1896, p. 544.

[3] *Zool. Anz.* XIX, 1896, p. 424.

[4] P.S. Since this paper was read Mr L. Doncaster, of King's College, Cambridge, has repeated the experiment on *Asellus* with the same result.

mittee are desirous of receiving returns made independently by different persons for the same district. It is of course hoped that returns may be obtained for districts in which the dark forms are still unknown. The secretary will be glad to examine and prepare descriptions of any illustrative specimens lent to him for that purpose, and in suitable cases arrangements will be made for photographing such specimens.

Historical Evidence. As the changes in question have largely taken place within living memory, it is hoped that those who have personal knowledge of the facts may be induced to put them on record in such detail as is still possible. Much information of a historical character is of course already printed in the scientific journals, but a more detailed account of the facts would be of great value. With this object a special schedule (B) marked "Historical" will be issued to those who will fill it up.

On publication full acknowledgment will be made of all help received. All communications should be addressed to the Secretary of the Evolution Committee, W. Bateson, Esq., F.R.S., Merton House, Grantchester, Cambridge.

BRITISH LEPIDOPTERA[1]

[*The Entomologist's Record*, 1900]

It is pleasant to write a few words in appreciation of the second volume of Mr J. W. Tutt's *British Lepidoptera*. Of the great utility of this work there can be no doubt whatever, and the punctual appearance of Vol. II will be a matter of general congratulation amongst naturalists.

Mr Tutt's work aims at being in the first place a complete collection of all that is as yet known of the natural history of the species dealt with. These books are no mere compilation, but in the fullest sense original treatises. No pains have been spared to get together everything that relates to the structure, distribution, variation, life-history, and habits of each form in its several stages. Many of the facts thus given are new, a large part being the results of the author's own direct observation. Moreover, much of the information here published has been communicated privately to Mr Tutt by his numerous correspondents, and the mass of facts given at first hand is thus greatly increased. This is especially the case in regard to the life-histories, which in very many instances have been worked through in minute detail by Mr Tutt and his coadjutors expressly for this book. Owing to the wide appeal which the author has made to living entomologists for such personal records, and to his laborious researches into the literature already printed, the books probably represent the sum of existing knowledge on the subjects contained.

It is a special charm of Mr Tutt's treatise that the reader has a comfortable sense that his author is giving him no scamped work. Everything capable of verification has been verified, and nothing is repeated in slovenly fashion unchecked. For such a work not only professed entomologists, but all naturalists who from time to time require precise information as to lepidoptera, will be grateful to Mr Tutt, and his books will be required in every working library of natural history. Nothing of the kind has hitherto been attempted, and by reference to them much searching and weary correspondence will be avoided.

[1] [This, and the two succeeding articles, were published as reviews of Vols. II–IV of *A Natural History of the British Lepidoptera* by J. W. Tutt. Ed.]

The present volume deals with the Psychides and part of the Lachneides. Whether the views adopted by Mr Tutt on questions of classification and the like are sound or not can, of course, only be judged by specialists, but it will be evident to any student of zoology that he has attacked these problems in a most fruitful way, and that in each of the numerous discussions of special questions he has provided a marshalling of the facts which will help succeeding students. Several sections of this kind are introduced relating to general questions of the morphology of lepidoptera, especially the nature of metamorphosis and the structure of pupæ. In addition to these there is an important chapter written by Dr T. A. Chapman on the phylogeny of the lepidopterous pupa, a subject on which he is the recognised authority.

In connection with the significance of larval moults, reference is made to the interesting observations of Chapman on variation in number of moults in *Arctia caia*, but there appears to be no account of Dyar's remarkable evidence relating to similar variations. According to Dyar's observations on several species, the larva—as measured by the width of the head—increases in size at each moult in a definite geometrical ratio, and when stages are added or omitted the ratio is halved or doubled accordingly. It is most desirable that further investigation of this curious phenomenon should be made, and it would have been well to direct the attention of students to the subject. It is noticeable that while morphologists, in reasoning based on developmental histories, have constant occasion to postulate intercalation or suppression of stages, almost no variations of this kind have yet been systematically observed. Those instances recorded in lepidoptera offer an unusually good field for research.

When an author has done so much for his readers it is a thankless task to find fault. Still one cannot help reflecting what a magnificent book this might have been if the mass of material here brought together had been fully digested and arranged. It is no doubt impossible for a very busy man to carry out such a task, and we are grateful for what is already done. But on turning over the pages it is sad to find a profusion of matter relating to questions of general scientific importance buried in the systematic chapters of both volumes, where probably they will never be seen by those who would most value them. To urge that these should have been extracted and printed together with the chapters on general morphology apart from the course of the systematic work is a counsel of perfection. Mr Tutt

will, however, greatly increase the gratitude of students if he will in the next volume provide a copious subject-index, which, though an arduous task for anyone else to perform, would cost him comparatively little labour. So long as merely the names of the insects are indexed as they occur, half the author's labour is in vain.

As another practical point it may be urged that the references should be more fully repeated. In a good many cases references to publication of notes or observations of a special character are not given with sufficient emphasis, and are only to be found by working through the profuse lists given under the heading "Synonymy." To remedy this is doubly important in a work where so much is taken from manuscript and other private sources. After a long hunt for the original source of a statement here given with a name of an authority affixed, it may prove at last that the statement was privately communicated to the author. In all such cases it should be plainly indicated that the authority was manuscript or verbal. This need not lengthen the book, and on the other hand space might be saved by cutting down some of the long lists of localities, which, in the case of generally distributed species, are hardly worth the considerable trouble they must have taken to prepare. It will be understood that these remarks are made in no unfriendly spirit, but simply in the hope that we may lose none of the benefits which Mr Tutt's industry has conferred upon us.

BRITISH LEPIDOPTERA[1]

[*The Entomologist's Record*, 1902]

THE third volume of Mr J. W. Tutt's *British Lepidoptera* is a really important book. It has been compiled on the same plan as the preceding volumes, though partly on account of the particular genera treated, but more from the catholic taste with which the author has brought together his materials, the present work is even more useful to the scientific entomologist than Vols. I and II. To the collector and systematist Mr Tutt's books are without doubt of high value. The analysis of specific and varietal characters is evidently made with extreme care, but, to the general naturalist, and especially to the student of evolution, the book has a direct and uncommon importance.

Nothing of this kind has been attempted in any language hitherto. Mr Tutt, though modestly entitling his work *A Natural History of British Lepidoptera*, has gone much further afield than such a title would lead a reader to expect. For example, in treating *Lasiocampa quercûs* we are provided not merely with a discussion of the British races, but an abstract is given of all that has been observed in the field or discovered by experimental breeding regarding the foreign forms and the laws which govern their heredity and variation. Again, in connection with the natural history of *Saturnia pavonia*, Mr Tutt introduces a full account of Standfuss' important experiments in crossing the Continental species. Many similar examples might be given illustrating the broad scope of the work.

It may well be imagined that in dealing thus liberally with species such as *quercûs*, *potatoria*, *pavonia*, *tiliae*, *populi*, and *ocellata*, all forms famous in the literature of variation and hybridisation, a very fine body of evidence has been amassed. To take the subject of gynandromorphism alone, it is scarcely too much to say that the raw material for a treatise is scattered through Mr Tutt's pages.

The abstracting and condensation of the evidence, so far as it can be judged by one who is not a professed entomologist, has been most carefully done, and the reader may feel confidence that, though the points are concisely put, exaggeration has been consistently avoided. Altogether, such a work is one to be thankful for, and there can be no

[1] [See note, p. 394. ED.]

doubt that such a publication will stimulate the younger generation of students to step from the narrow track of mere collecting and to wander off into the more fertile fields of experiment and observation of living forms.

When so much has been done for us criticism is hardly in place, yet a reviewer can scarcely avoid repeating a word of regret that the author has not leisure to digest his materials rather more completely. The trained student knows what to expect under the head of *quercûs*, *populi*, and the like. He will easily find his way to the matter he is seeking, but even a professed naturalist, who had not a fairly clear idea beforehand of the class of fact each species was likely to provide, might find a good deal of difficulty in using the book. The kind of organised arrangement called for is, unhappily, about the most exacting task an author can set himself, and many a fastidious writer has never published his collections at all because he had not the opportunity to arrange them ideally. Let us be grateful to Mr Tutt that he at least has not sinned that barren sin.

A subject-index would go far to put all this right. Mr Tutt tells us in his preface that if anyone will make such an index, he will print it in the next volume. Cannot some keen young worker take him at his word? Meanwhile, the student of evolution must not be daunted by the difficulty of putting his hand at once on the fact he is looking for, and the physiological *chiffonnier*, as Claude Bernard called himself, may be assured that if he will only rummage about a little, he will pick up some rare treasures in Mr Tutt's heap.

To include everything that can by any possibility relate to, or interest the student of the British fauna, is to err on the right side, though the connection with that fauna be rather remote. Now and again, however, we come on a few pages which are very doubtful in point. Space being so valuable, we feel that, for instance, the details regarding the structure and classification of the Attacides of the world need not have found a place here, not that the facts are unimportant, but no one is likely to look for them in a work on a fauna which contains one solitary species of the group.

The unprofessional reader wonders, too, who *uses* the solid pages of locality-records in the case of species widely distributed. When these records detail the varieties of the districts, their value is manifest, and they will form a solid basis for the observation of future changes in distribution. Did we not feel sure that, in this case, the author knows the requirements of his public, we might be disposed to ques-

tion whether this was really the best use to which the labour and space could have been put.

None of these remarks, however, detract from the statement that the new *British Lepidoptera* is a fine scholarly piece of work, for which not only the entomological specialist, but naturalists of all orders will be thankful to Mr Tutt for many a year.

A NATURAL HISTORY OF THE BRITISH LEPIDOPTERA[1]

[*The Entomologist's Record*, 1904]

A SLIGHT delay in the publication of Vol. IV of Mr Tutt's important work was necessary, in order to enable Mr G. Wheeler to prepare the synopses of this volume, and to complete the general index to the four volumes now published. All who use the book will be grateful to Mr Wheeler for these valuable additions to the work, but, perhaps, the obligation will be most felt by those who, like the present writer, without being professed entomologists, have frequent occasion to refer to entomological evidence. On previous occasions attention was called to the importance of Mr Tutt's collections of facts relating to hybridity, variation, and other phenomena of great general interest, records hitherto for the most part hidden by masses of information which only the specialist will read. By Mr Wheeler's labours these difficulties are now removed, and, as a work of reference, the utility of the book is vastly increased. The high qualities which characterised the earlier volumes are present equally in the new one. Each species is treated with the thoroughness that Mr Tutt and his collaborators always bring to bear on the subjects they undertake. Whenever possible the several instars of development from egg to imago have been examined afresh for this work, and every departure from normality is minutely described. The lepidoptera offer unique opportunities for such studies in developmental variation, but never before have they been used on so comprehensive a scale. Morphologists have long devoted themselves to the precise study of developmental histories. The phylogenetic significance of every feature has been repeatedly discussed, the freest assumptions being made as to the manner of omission or intercalation of stages. But though in lepidoptera such omissions and intercalations may very readily be witnessed as actual variations, embryologists have but seldom given attention to these facts. We cannot doubt that the appearance of Mr Tutt's treatises will do much to promote the study of such suggestive phenomena, and lead to a further recognition of their bearing on the problems of development and evolution of types. Every fact yet ascertained respecting the structure, physiology, and mode of occurrence of each species is given with the utmost detail, so that the

[1] [See note, p. 394. ED.]

work has become rather a series of monographs than a handbook. The biologist who requires a summary of all that is known regarding most subjects—as the polymorphism of the larva in *euphorbiae* or *atropos*, the invariability and singular habits of the imago of *stellatarum*, the modes of oviposition, the production of the "squeak" of *atropos*, the seasonal phenomena of immigrating forms—may go to the new *British Lepidoptera*, with the certainty that he will there find everything that is known up to the date of publication, accurately compiled and set forth.

Of all these points Mr Tutt has done well to err on the side of inclusion, even if some prolixity result. The student, with the help of Mr Wheeler's synopses and index, can now find his way to what he wants to know. But, as volume succeeds volume, the conviction grows that the profusion of detail which has a use where genuine problems and little-studied points of physiology are concerned, is meaningless in the case of capture-records and locality-lists for cosmopolitan species. It is not in a spirit of criticism, but in the genuine desire to further his magnificent undertaking, that I appeal to Mr Tutt on this question. The present volume deals with twelve species in 471 pp. Of these no less than 74 pp. are occupied with closely printed matter which I find it impossible to suppose that any one will ever read. For *stellatarum* and *convolvuli*, admittedly cosmopolitan, I find 9 pp. of solid brevier type, giving localities alone, which might as well be the index of a Gazetteer for any scientific purpose they will serve. All this information had to be collected, written, set, corrected, and printed. Surely the time of an able and very busy man would have been better spent in dealing with the essential features of the two or three more species which these lists crowd out.

Every naturalist must hope that Mr Tutt may be enabled to deal with at least the most important of the groups as yet untouched. In the new preface he states, what is but too true, that, at the present rate, this hope can never be fulfilled. Yet much might be done by the substitution of summaries for these portentous lists of places and dates, to the great profit of entomological science. Had this course been followed from the first, we might now be expecting shortly to receive Vol. v. Would not the list of subscribers feel a certain benefit also?

Where scientific judgment is concerned, Mr Tutt's treatment has every appearance of soundness. In his revision of the Eumorphinæ, he comes to the conclusion that the seven British species are out-

lying representatives of four distinct tribes. This is a point on which only specialists can profess to judge, though since we are informed that Messrs Rothschild and Jordan have made independently the same decision, this coincidence of testimony may be taken as decisive. Further, in Mr Tutt's opinion, each of our own species should be regarded as of a separate genus. Now there may be marked points of difference, but if all animals and plants were judged by similar criteria, union into genera would probably have to be abandoned, as serving no useful purpose. Whatever may be held regarding species, it may now, I believe, be conceded that generic units have no recognisable physiological or evolutionary meaning. Generic names bring together species which have so much in common, that it is convenient to think of them habitually in association, leaving their differences to be sufficiently emphasised by the specific names. These groupings have no natural significance *definite enough for general recognition*. It is, therefore, surely best in every case of doubt to maintain, rather than to subdivide, genera, lest we come to have two names where one is enough.

A considerable section of the book is devoted to a recital of the facts regarding alleged hybrids between the various Eumorphids. Mr Tutt states that in only one of these instances has it been declared that the actual pairing of the two species (*elpenor* and *porcellus*) has been observed, and this case he doubts. He is certainly right in insisting on caution before accepting as evidence of hybridisation phenomena which may well be variational. But, after examining the evidence he has collected, I can find no clear reason for deciding, as Mr Tutt does, *against* the hybridisation view. Pending experiment, the nature of these cases should be regarded as simply problematical. I have an impression that Mr Tutt's bias is here determined partly by his judgment on the question of generic subdivision. Nevertheless, the hypothesis that the so-called hybrids are variations connecting the two putative parental forms, somewhat weakens the emphasis laid on the generic distinctions. Moreover, as Mr Tutt is doubtless well aware, there are many groups, both of animals and plants, in which hybrids occur between types, which all of us agree should be treated as generically distinct. The successful continuation of Mr Tutt's book is so important to entomology, and especially evolutionary science, for which it contains the raw material in plenty, that I trust both he and his collaborators will give earnest consideration to the recommendation made above. Every page unnecessarily included delays the

progress of the whole and tends to obscure its high scientific qualities. If a wise course of compression be followed, we may look forward to acquiring, within a reasonable time, a treatise which will be nothing less than a *corpus* of human knowledge respecting the natural history of British lepidoptera. Such a work will rapidly make itself known, and must infallibly find its way to every scientific library.

HEREDITY, DIFFERENTIATION, AND OTHER CONCEPTIONS OF BIOLOGY: A CONSIDERATION OF PROFESSOR KARL PEARSON'S PAPER "ON THE PRINCIPLE OF HOMOTYPOSIS"

[*Proceedings of the Royal Society*, LXIX, 1901]

In his paper on *Homotyposis*[1] of which an abstract appeared in the *Roy. Soc. Proc.* vol. LXVIII, p. 1, Prof. Pearson raises an issue of extraordinary importance. In any attempt to perceive the true relation of variation to differentiation, and to analyse the essential similitude existing between Heredity and Repetition of Parts, we reach a fundamental problem of biology. Little has thus far been done towards elucidating this problem or even towards formulating it. The appearance of Prof. Pearson's remarkable memoir may perhaps therefore with profit be taken as an occasion for considering critically some aspects of these questions.

It is impossible to write of Prof. Pearson's paper without expressing a sense of the extraordinary effort which has gone to its production and of the ingenuity it displays. But on careful examination it will, I think, be seen that in the light of known facts there is serious doubt whether the determination of what Prof. Pearson calls the average homotyposis of "undifferentiated like parts" can be attained by his observations, and that there is even graver doubt whether, if it were attainable, such a value would have any natural significance. In the course of this consideration it must, I think, also appear that the comparison he attempts between the average homotyposis of "undifferentiated like parts" and average fraternal correlation in families is incorrectly instituted.

At the outset I wish to express the conviction that the leading idea which inspired and runs through the work is a true one. Prof. Pearson suggests that the relationship and likeness between two brothers is an expression of the same phenomenon as the relationship and likeness between two leaves on the same tree, between the scales on a moth's wing, the petals of a flower, and between repeated parts generally. The conception of heredity is thus greatly simplified, and that phenomenon is seen in its true relation to the other phenomena of life, becoming merely a special case of the phenomenon of Division and repetition of parts.

[1] *Phil. Trans.*, A, 1901, vol. 197, p. 285.

This idea came first to me—as it has perhaps to others—when I was studying the phenomena of Variation in Meristic Series, and in writing on that subject I introduced an outline of the conceptions involved[1]. On that occasion I ventured to carry this reasoning a step further, as it seemed, and to suggest that *the resemblance which we call Heredity may be a special case of the phenomenon of Symmetry.* The thought then expressed has been a constant companion ever since, and I have become more and more convinced that it is fundamentally true.

I should welcome Professor Pearson's paper inasmuch as it is an attempt—the only one, so far as I know—to emphasise and develop this conception; for, like him, I am sure that it may provide the key to the nature of heredity, perhaps also to problems beyond.

Variation in some of its essential features may thus perhaps be reduced to a geometrical problem. One of the many factors or conditions of fraternal resemblance may be Symmetry of division, quantitative and qualitative. The reference to the phenomenon of Symmetry seemed to me to carry the principle a stage further, and to show Heredity as a special case of a phenomenon, the conditions of which we may reasonably hope, in a measure, to apprehend in at least its simpler phases. Prof. Pearson, on the contrary, avoids mention of Symmetry. This arises, I presume, from a desire to use a more general expression, and from a reluctance to appear to exclude from his comparison the relation between members of Linear or Successive Series, whose mutual relationship is not one of Symmetry in the ordinary sense. He would probably prefer to regard Symmetrical division as a phase or perhaps as a consequence of the phenomenon of the production of "undifferentiated like parts" occurring under special conditions.

I still think something is gained by inverting the statement and speaking of the likeness between the parts as a phenomenon of Symmetry. In some respects Prof. Pearson's mode of expression is preferable as being more comprehensive, but mine has the advantage of keeping before the mind the fact that it is in the *Symmetry of cell-division* that the *resemblance* between relatives is presented in its simplest form; and also that the axes along which the "like parts" are produced are frequently definite.

[1] For a somewhat fuller treatment see *Materials for the Study of Variation*, 1894, Introd. Sect. VII [p. 254, *supra*]; and also p. 21.

Thus, fraternal correlation in its most striking manifestation is seen n the simultaneous variations of Homologous Twins[1].

It is true that the geometrical relations of members in Successive Series are not included in the term Symmetry[2], but the distinction is largely one of degree, and the transmission from one to the other is of frequent occurrence. Similar organs may be repeated in one species in radial series, while in an allied species the same organs by differentiation of an axis stand in succession to each other, as every naturalist knows.

Prof. Pearson writes (p. 291): "When we ascertain the sources of variation in the individual, then we shall have light on the problem of fraternal resemblance." May we not also say that when we ascertain the conditions of asymmetrical division we shall have light on the problem of fraternal variation?

I introduce this reference to my own method of expression partly to show how far I am in agreement with Prof. Pearson on a main point, and partly to emphasise the significance which the analogy between Repetition and reproduction gains by the reference to Symmetry.

Theoretical considerations in mathematical form are put forward by Prof. Pearson as tending to the belief that the numerical value for homotypic correlation will, on an average of cases, approximate to the average value found for fraternal correlation.

The reasoning is beyond me, but I gather that the argument, by the introduction of approximate assumptions, amounts to a proof that if the characters of the offspring as measured, by their deviations, depend on those of the germ-cells of the parents, then the characters of the repeated parts (or *undifferentiated like* parts) formed by that offspring will similarly depend on those of the germ-cells; and it would then be expected that the correlation between those repeated parts of the same individual would be similar in intensity to that between the germ-cells of its parents. Whether the assumptions are justifiable I am not able to judge, as I do not properly understand them.

[1] See *Materials*, pp. 559 and 560. Following the work of Driesch and others on the artificial production of Double Monsters, we must regard the relation between Homologous Twins as of the same nature as that subsisting between the right and left halves of a bilateral organism.

[2] It would be easy to suggest terms better adapted to the expression of these conceptions, but to do this at present is premature. When it becomes necessary to do so I anticipate that the largely analogous phenomena of rhythmical vibration will provide ready metaphors from which to construct a terminology well adapted to denote the various phenomena of Merism.

The resemblance or correlation between "undifferentiated like parts" is, then, regarded as a phenomenon similar to the correlation between brothers. The latter correlation has been investigated by Prof. Pearson in a number of heterogeneous cases, and has been found to vary from ·1973 to ·6934, where 0 is zero and 1 denotes complete correlation[1]. The mean value approaches ·45. He proposes in this paper to find a numerical value for the average correlation between undifferentiated like parts of the same individual. A large series of heterogeneous cases of various organs in various plants have been investigated. The values found range from ·1733 to ·8607. Reasons are put forward for excluding some of the highest and for doubting the validity of others, especially some of the lower ones. Eventually the average result ·45 is again reached, taken on a series ranging from ·1733 to ·6311.

Prof. Pearson attaches importance to the rather close similarity between the two average values. We are bound, therefore, to remark as a suspicious circumstance that the range of values is so wide, and that the average value should so nearly approach the mean of the whole possible range; but upon this point I do not propose to dwell, preferring to deal with more general aspects of the problem.

Now Prof. Pearson is attempting to measure to what extent there is a resemblance or correlation between repeated parts of one individual as compared with the same parts of different individuals of the same race: how much, that is, of the resemblance between repeated parts of an individual is due to its individuality? Further, how much on an average of many individuals may be expected to be due to individuality?

For various sources of error Prof. Pearson is well prepared. In his *Malva* material, for instance, he finds little correlation due to individuality; because, as he points out, his specimens may have been all or largely the vegetative produce of one or few individuals. In some mushrooms, on the contrary, he finds this correlation high, but he thinks that here individuality may partly be due to stages of growth, for his individuals were not all of similar age. In comparison with what follows these sources of error are trifling.

It will be remembered that the series of homotypes is to be *undifferentiated*. If differentiation exists and is not recognised the apparent homotyposis due to individuality will, as Prof. Pearson perceives,

[1] Both here and in the coefficients of "homotyposis" reasons are given for supposing that some of the greater departures from the mean may be explained away.

be immediately lowered. In order, therefore, that the inquiry should have significance, it is necessary that differentiation occurring between members of a series of parts should have a clear meaning as distinct from variation occurring amongst them; and further, in order that the investigation should be carried through, we must be able to discriminate such differentiation from variation. On critical consideration it will be apparent that neither of these postulates accords with the facts of nature. I cannot find that Prof. Pearson has in any real way dealt with this difficulty. The practical difficulty he has perceived and in part met, but the more serious theoretical difficulty has, I think, escaped him. When fully understood, it will surely be seen to invalidate the whole argument.

Let us grant for the moment that differentiation of the parts can be dealt with—if it can be detected; but if differentiation occurs in different individuals in different degrees and directions, how can it be told whether the ensuing deviations in correlation are due to a change in the control of individuality over the variation, or to irregular and incipient differentiation? Yet, is not such differentiation exactly what is to be expected in the variation of homotypes? Do not most animals and plants exhibit this phenomenon, and must we not believe that these organisms have attained their present forms largely by variations among their repeated parts? In view of these familiar facts, can Prof. Pearson point to any feature which positively distinguishes variation occurring between members of a series from differentiation?

That differentiation may in practice be mistaken for variation between homotypes he is aware. It is not, however, the difficulty of recognition I would now emphasise, but the fact that between the two phenomena no absolute distinction exists in nature. An "undifferentiated series of like parts" means only a series of like parts which have varied and are varying among themselves but little. A series of highly valuable like parts is a series in which differentiation exists or is beginning to exist in a complex and irregular fashion. A "differentiated series of like parts" means a series among which variation is or has become definite and regular. Between these classes there is every shade and degree. No one can say finally where each begins and ends, and, by appropriate selection, we could find homotypic coefficients of any required value. The *average* value of such coefficients taken at random has no significance in nature.

Let us examine some practical examples.

In Prof. Pearson's *Nigella*, for example, the correlation between the numbers of segments in the capsules of individual plants is found to be low. That is to say, given one seed-vessel of the plant, it will give you very little information as to the most probable number of segments in a second seed-vessel of the same plant. Why is this?

From the look of the plant, or, if such simple perceptions are mistrusted, by counting the segments of seed-vessels on lateral branches, and comparing the numbers obtained with those obtained from seed-vessels borne on central axes only, it is easy to show, as Prof. Pearson points out, that the numbers are generally lower in the case of the laterals. We recognise, further, that the proportion of laterals varies from plant to plant.

How is the differentiation detected in *Nigella*? By the *regularity* with which small capsules are associated with lateral branches.

But suppose that for any reason this regularity were masked, should we then perceive the differentiation? Might it not pass, wholly unsuspected, for a change in correlation? Undoubtedly it might.

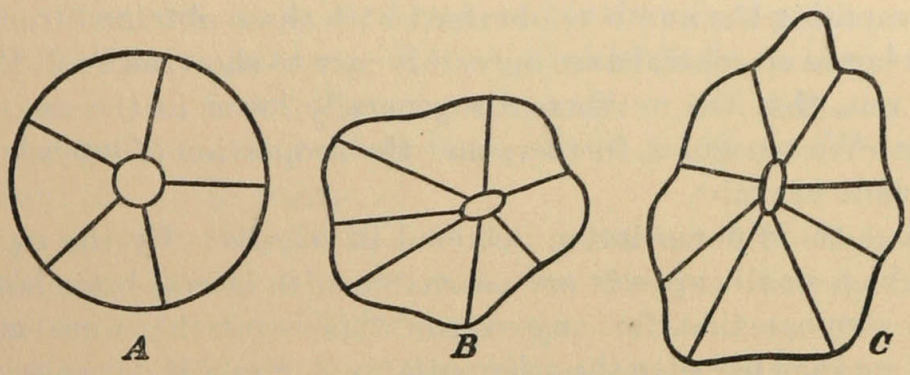
Take the case of blood-corpuscles of a frog. Measure some character of a hundred corpuscles in each of many frogs. Find the correlation due to the individuality of the frog. How can we determine whether in some of the individuals we have used there may not be differentiation such as was found in *Nigella*, so that the parts are not really "undifferentiated like parts"? Would not such irregular differentiation change the mean correlation between the corpuscles?

Would not the fear of such an error practically lead to the exclusion of cases of suspected differentiation *which ought to be included* in calculating the average? Is it not certain that differentiation in important characters may take place in exactly the masked way I have referred to? If, for instance, we could count granules in the corpuscles and work out their homotypic correlation for these numbers, might not we have among our individuals some which had specialised corpuscles absent in others?

Again, does not individuality show itself by *change in the degree* of differentiation among homotypes? Can we frame a definition of variation which will exclude such changes?

A represents a radially symmetrical organism in which we may study the correlation in lengths of the radial septa and determine how much is individual or homotypic, and how much racial. If the radial symmetry were always perfect and the specimens merely of different sizes, the racial and homotypic correlations would be alike, unity.

But suppose the population consists partly of (i) approximately radially symmetrical specimens; (ii) quite irregular specimens like B; (iii) of specimens whose forms are controlled by an incipient differentiation of any axis tending towards such a form as C^1. How would Prof. Pearson's methods determine the true homotypic correlation in this population?



Suppose that in a polychaet, say a Syllid, there is marked differentiation between segments at the anterior and posterior ends separated by hundreds of segments apparently undifferentiated, bearing appendages similarly undifferentiated. We may determine the homotypic correlation of these appendages. So long as differentiation regularly and conspicuously begins at a certain region we can exclude it. But suppose in some individuals it begins at one segment and in another at another, as it almost certainly would do, how should we know which specimens or which segments must be rejected as introducing a confusion through differentiation, and which must be included in reckoning homotypic variation? If differentiation is irregular, will it not change the apparent homotypic correlation?

Prof. Pearson has determined the racial correlation for the lengths of the first phalanges of digits III and IV in women. It comes out high, ·914[2], as might fairly be expected by any one who had studied the meristic variations of digits. There is, of course, differentiation between these two digits, so that they may be said to be unsuitable subjects for determination of homotypic correlation of like parts. But if instead of man, the digits III and IV had been studied in an Artiodactyle, say a deer, the *racial* correlation would doubtless have been much nearer unity. In other words, these two digits in the deer

[1] I have no doubt that a study of the corals, say, would provide actual examples of such a population. May not some mushrooms be in just this state?

[2] *Grammar of Science*, 1900, p. 389.

are approximately in the relation of bilateral symmetry about the median axis of the foot.

In this case the differentiation between the digits is low. They approach the homotypic condition, and their homotyposis could be measured. But a population may consist of some individuals in which there is a high correlation between these two digits III and IV, and others in which differentiation had begun or sensibly persisted. In such a population the racial correlation would be clearly reduced. But would not the homotypic correlation, as calculated, be changed also? Would Prof. Pearson's method show to what extent incipient differentiation had introduced error in the determination of the homotypic correlation[1]?

Yet another and even clearer illustration. The two claws of a crab are a pair of homotypes. Their homotypic correlation in respect of any character, length for example, might be determined. Now there are species of crab in which the two claws are approximately equal or undifferentiated. On the contrary, in some species the right, in others the left, in others the right or left with varying frequency, is differentiated in size and other characters. Can it be decided in such a case which deviations from, or approaches to, bilateral symmetry are, *as variations*, to be included in a determination of homotypic correlation, and which are to be rejected as due to changes in differentiation?

On this rather wider view of the facts is it not manifest that the distinction rests on fallacy? The reality of the problem as defined by Prof. Pearson depends on the assumption that there is an absolute distinction between differentiation and varying among repeated parts, and its solubility depends on the assumption that this distinction can be perceived. The proviso that such a distinction is to be observed stultifies the whole inquiry. So far are we from being able to perceive this distinction, that we may even doubt whether variation among repeated parts *can* take place except as differentiation. If the idea of variation is to be extended to the case of differences between repeated parts it must inevitably include differentiations among them.

But, unless differentiation can always be detected or always reckoned for, the *average* value of the homotyposis coefficient will have no more natural significance than would the average variability

[1] If Prof. Pearson declares that such differentiation would be "statistically discoverable," he must assume that the differentiation would always affect the same digit in the same direction, an assumption for which I can see no warrant.

of all organisms measured by their "Standard Deviation" from their various means, or the average size of living cells, or the average weight of all ponderable bodies.

I now proceed to a different point, in a sense the converse of the former. Prof. Pearson perceives that the correlation between "undifferentiated like parts" has an analogy with the resemblance or correlation between brothers. But does he recognise that variation between brothers is comparable not merely with variation between repeated parts, *but also with differentiation*, and with predominantly orderly variation among such parts? The phenomena in a colonial or social form will clearly illustrate this principle. Ova and spermatozoa may be treated as "undifferentiated like parts" so long as their variations, judged by the resulting offspring, are sensibly irregular. Can we recognise differentiation among them as distinct from variation? Certainly we *sometimes* can. In determining the correlation of confraternities, the parentage enables us to distinguish the fraternal groups correctly, and consequently a fraternal correlation may be truly determined. *For to do so we are not compelled to distinguish differentiation from variation.*

But I put it that the parallel Prof. Pearson is seeking is improperly instituted in his paper. He compares the homotyposis of "undifferentiated like parts" with the correlation between brothers. *He ought to compare it with the correlation between undifferentiated like brothers.* As it is, he is trying to find for homotypes what he would be trying to find if he set about a determination of the average value of fraternal correlation for fraternal groups of *like members taken from families composed of differentiated members.* Such an attempt would immediately necessitate a distinction between differentiation and variation. Had his comparison been correctly instituted, Prof. Pearson could hardly have failed to discover the fallacy on which I submit his reasoning is based.

Let me state a case in illustration. In most species of ants, females are differentiated into workers and queens. Frequently other castes, soldiers and others, are similarly recognisable. As regards formulation of his problem, Prof. Pearson will perceive that the parallel to average homotyposis is *not* average fraternal correlation of even all the females from one pair of parents, but the correlation between workers, or between soldiers, etc., of one family. He may reply that this objection, though true on the point of form, can be met by weighting the various castes when they are compared. I doubt whether

the difficulty is thus fully met (even if in practice it were possible to carry out the process). Should we even then be comparing comparables?

Should we not still be finding a correlation like that for a miscellany of *differentiated* series of repeated parts?

This reasoning, so clear in the case of ants, extends to all cases of differentiation between members of confraternities.

To find then a value comparable with the homotyposis of *undifferentiated like* parts we must find the fraternal correlation between *undifferentiated like* brothers. But differentiation has here again no meaning which can be determined with precision. It shades insensibly into variation.

Suppose we merely propose to determine the *average* value of fraternal correlation in *workers* of one genus of ants. In some species we sort our ants easily into workers and the rest. In another species we shall find differentiation so imperfect that we cannot say for certain which are soldiers and which workers. Finally, even in the more completely differentiated species we shall find occasional nests (families) which show an imperfect differentiation[1]. Average fraternal correlation, I think, has no meaning, still less an ascertainable value, in these cases.

The principle that Prof. Pearson calls "homotyposis" I have expressed by the statement that the variations of parts, repeated in series, *may* be "similar and simultaneous[2]." Beyond this we cannot yet go. Prof. Pearson's statement of the principle fails to recognise one of the most important features of homotyposis. Expressed in my own terms, Prof. Pearson's "homotyposis" is the principle of "similar and simultaneous variation" restricted to *undifferentiated like parts*.

But relationship is not lost when we pass to the differentiated parts, and such differentiated parts *may* vary similarly and simultaneously with other differentiated parts of the same series, exhibiting the phenomenon of Homœosis. A stamen of a rose, if it becomes petaloid, is not merely a petal, but *a petal of the individual* rose it is on. Prof. Pearson's principle, as stated by him, misses this point.

If he had correctly instituted the comparison between parts and individuals he would have seen this also. For in cases of confraternities he must be familiar with the phenomenon of similar variations

[1] See the writings of Forel.

[2] *Materials*, p. 569.

occurring simultaneously in separate groups of differentiated members.

But let us now suppose we could define differentiation from variation in general, say, as orderly variation. Even so we could not distinguish it unless its order were conspicuous. In a former paper[1], Prof. Pearson wrote that "the very nature of the distribution of variation, whether healthy or morbid, seems to indicate that we are dealing with the sphere of indefinitely numerous small causes, which in so many other instances has shown itself only amenable to the calculus of chance, and not to any analysis of the individual instance." As I have on many occasions stated, such a description accords ill with the observed facts of variation. Illustrations to the contrary are numerous and are now becoming familiar; and even in Prof. Pearson's later works references to them are not wanting.

Does not, then, the presence of orderly differentiation, in various degrees, *compel* us to an analysis of individual instances? In plain language, we shall have to pick and choose our cases, and the value of our coefficient of homotyposis will depend entirely on how we do it. Has not Prof. Pearson himself been so compelled in more than one of his examples, notably in that of *Nigella*? Has he any certainty that such an analysis ought not to have been made in other examples also?

He speaks of the extreme difficulty of determining whether his material is homogeneous in respect of environment, but I miss from his work any deep appreciation of the subtle and evasive quality of differentiation. If any one would obtain a conception of this difficulty let him go to any tree or large plant and set about pruning it, or better, let him try to choose shoots for propagation. Until he tries, it seems simple enough; but when he begins he finds the shoots are of many complexly differing kinds, and unless he has experience of pruning or of propagation, he will not know which to choose. If he studies the tree attentively, he will soon see that the kinds of shoots are largely definite and, in fact, differentiated. The differentiation may be irregular or regular. That of the leaves may or may not be correlated with that of the shoots. The differentiations may be correlated with the age of the wood, with the absolute size of the tree, they may be peculiar to the variety, or they may be individual to the specimen and defy analysis[2].

[1] *Phil. Trans.*, A, 1896, vol. 187, p. 255.

[2] There are examples not only of differentiations occurring irregularly in one species

I am of course aware that Prof. Pearson knows all this, but I gather the impression that he regards these differentiations as largely recognisable and capable of exclusion. He may hope too that by increasing the area of his statistics these orderly disturbances may cancel each other. This appears to me highly improbable.

Order in occurrence is generally the only indication of differentiation, and when the order is observed, differentiation may pass wholly unobserved. But the presence of such differentiation will vitiate the result, even if the area of statistics be indefinitely increased.

The only answer which seems open is that though it may be impossible to define precisely in words which examples should be reckoned in determining average homotypic correlation, and which must be excluded as showing differentiation, yet in practice the difficulty is not a real one, and that divers features (*e.g.*, regularity of occurrence) enable us to detect sensible differentiation[1].

Such an answer is far from covering the whole ground of the objections I have indicated, as may readily be seen by attempting to apply it in the practical illustrations given above. But besides this, to take that ground would be to turn back from that appeal to rigid numerical treatment, which Prof. Pearson has told us should be the sole test of these hypotheses.

I may further point out that if it were suggested that the distinction between differentiation and variation may be left to the judgment of the observer; we might by a similar exercise of judgment attempt a distinction of variations into evolutionary or *specific*, and *normal*.

This is far more than a merely logical point. I am disposed to think that such a rough classification boldly made and carried out for a number of familiar forms might greatly promote the study of evolution, even though no precise criterion can yet be provided. This suggestion will be abhorrent to many naturalists, though for want of such a distinction much of the statistical work produced by Prof. Pearson and his followers has, I believe, gone wide of its mark, if that aim is the elucidation of Evolution. More fitly might this work be described as "Mathematical Contributions to a Theory of Normality."

and regularly in another, but also of the separation of these very forms of differentiation as characteristics of distinct varieties. See for instance the heterophyllous junipers and cypresses.

[1] Prof. Pearson's reference to *Nigella* (p. 320) as unsuited to his purpose because probably "*unstable*" suggests to me he had here this difficulty in view.

In the treatises I have referred to Prof. Pearson is seeking for a statistical conception of species through an examination of miscellaneous variations. The impression left on my mind by such imperfect study of his works as I have been able to make, and especially by the present paper, is that the evidence points to some conception of normality to be otherwise attained, a conception more finite and concrete than any we have yet reached.

By the one word *Variation* we are attempting to express a great diversity of phenomena in their essence distinct though merging insensibly with each other. The attempt to treat or study them as similar is leading to utter confusion in the study of evolution[1].

If normality thus imagined can be shown to be a real phenomenon, it is conceivable that we might then profitably attempt to determine in specified cases the average value of homotypic correlation for each case, but the average value for a miscellaneous collection of cases would still have no natural significance.

(*Note, added November*, 1901)

On p. 287 Prof. Pearson has added a note in which he seeks to meet a part of my objections. He says: "A diversity due to differentiation and a variability due to chance are quite distinct things. The one is the result of dominating factors which can be isolated and described; the other of a great number of small factors, varying from organ to organ, and incapable of being defined or specified. Indeed, upon each dominating factor of differentiation is superposed such a chance variability. Of course all things which differ even by chance variation are in a certain sense differentiated." This welcome passage outlines the conception that must form the point of departure in any attempt to understand variation in its relation to Evolution. The same conception I have myself often laboured to express. On former occasions to these two kinds of diversity of which Prof. Pearson speaks I have applied the terms "Discontinuous" and "Continuous." Though useful in practice, those terms are open to misconstruction and perversion. In the present paper I have suggested the nearly equivalent terms "Specific" and "Normal." Similarly, to variations occurring among repeated parts or homotypes we might apply the terms "Differen-

[1] For example, in his criticisms (p. 360 and elsewhere) of the view that sexually produced offspring are more variable than offspring not sexually produced, Prof. Pearson is merely confusing different kinds of variations and applying to certain kinds conclusions derived from a study of another kind.

tiant" and "Normal." Throughout nature the variations between the members of fraternities may be discontinuous and specific, and in like manner may the variations between repeated parts be specific and differentiant, though in both classes normal or continuous variations are always superposed on them.

In most cases the naturalist is seldom in much doubt with which he is dealing. But though these two great classes of variation can broadly be recognised and treated as distinct, the distinction may be evasive, and when the differentiation is irregular that distinction must often be obscured and not "statistically discoverable." Prof. Pearson is mistaken in supposing that such differentiation must show itself in his seriations. It may appear *only* as a lowering of correlation. The diversity due to differentiation may exhibit a "homogeneous chance distribution," as, for example, in my illustration of the crab's claws. We have only to suppose that the "mode" of the population falls on a form with claws approximately equal, and—to take the simplest case—that the frequency of both right-handed and left-handed differentiation is inversely proportional to the magnitude of the differentiation, a state of things common enough in nature.

As a matter of fact even in the case of *Nigella* (p. 320) differentiation was detected not by the seriations, but by common observation. When the differentiation has been once detected, its influence can be seen in the seriations. This is a mere accident. If the material had happened to contain a certain proportion of a second race with a "mode" on 10 or 13 and a secondary "mode" on 8—a condition familiar in plants (from F. Ludwig's beautiful researches)—the differentiation might have been completely masked in the seriations[1]. As it is, the seriations alone contain nothing which *prove* the existence of differentiation. We happen to know otherwise that high numbers are associated with centrals and lower numbers with laterals. This is not revealed by the seriations. For all they show, the irregular distribution might be due to ordinary discontinuous variation obeying the laws which F. Ludwig has shown such distributions commonly obey.

We can feel nothing but admiration for those statistical methods which, as perfected by Prof. Pearson, are yielding many useful results not otherwise attainable, yet their limitations must be constantly remembered. But even if the differentiation could be discovered by

[1] I strongly suspect that something of this kind may actually exist in the case of Shirley Poppies.

these means, in eliminating it we should have arbitrarily excluded a class of facts which ought to have been included in calculating *average* homotyposis, or the correlation due on an average of cases to individuality. In determining the *average* correlation between brothers we must bring to account the continuous and the discontinuous alike: so in the *average* of homotypic correlations must be included both the differentiant and the normal alike.

To state the issue in a word: it appears that the attempt to exclude differentiation by definition must constantly fail in practice and is inadmissible in theory.

VARIATION AND DIFFERENTIATION IN PARTS AND BRETHREN

I. *Discontinuity and Definition*

For various reasons which need not be detailed, I have delayed a reply to Prof. Pearson's article "On the Fundamental Conceptions of Biology[1]."

His argument may be divided into two parts. In the first, he denounces generally the belief in discontinuity, as a main factor in evolution, and particularly my presentation of this belief; in the second, he makes a defence of the biometrical methods, and especially of that conception of average Homotyposis which was the original subject of our discussion. After a suitable delay I prepared a reply dealing with these various topics. I there attempted to elucidate and extend the conception of discontinuity, showing by appeal to the facts both what it implies and what it does not imply, and the degree to which some recognition of discontinuity is inevitable. On completion, this essay far exceeded the space which I could ask the editors of *Biometrika* to allot to me, and I am therefore compelled to curtail the general discussion, and limit myself almost entirely to the question of Homotyposis. With regard to one point however, that neglect of definition on my part, which Prof. Pearson has made a prominent subject of his strictures, I shall briefly indicate the lines of my defence, reserving the rest for another occasion.

The complaint which Prof. Pearson reiterates with the greatest vehemence is that in urging the significance of discontinuity in evolution I avoided direct definition of that conception, and even used the same term with various shades of meaning. The charge suggests that this vagueness was due to inadvertence, to some deficiency of logical sense on my part, and to general failure to reach a right standard of precision. Now, however reprehensible, this absence of definition was due, not to carelessness, but to design. Ten years ago, in introducing the question of Continuity and Discontinuity, I wrote as follows:

> And though for many a conception has no value till it be cast in some finite mould, my aim will be rather to describe than to define the meaning of the term Continuity as applied to Variation. In dealing with a subject

[1] *Biometrika*, 1902, I, p. 320.

of this obscurity, where the outlines are doubtful, an exact mapping of the facts cannot be made and ought not to be attempted; but I trust that from the present indications, vague though they are, some larger and more definite conception of Discontinuity in Variation may shape itself hereafter by a process of natural growth. For this reason I shall as far as possible avail myself of examples rather than of general expressions, whether inclusive or exclusive. (*Materials*, p. 36.)

Has not the reserve there shown found its fullest justification? Has not time brought exactly that "larger and more definite conception of Discontinuity" in Variation, which ten years ago it was impossible to form? Variation was then an empty name. Should I have pretended to define conceptions half-formed?

Prof. Pearson reproaches me that my "whole thought seems in flux"; I am happy to think that that was true. Did I profess it otherwise? Does Prof. Pearson consider plasticity a disqualifying condition in the mind of an inquirer feeling his way into a new study? Such an one will not go wrong if he take "a fair allowance of way, with honest liberty and prudence to his guard"; nor need he "pare that liberal path into a razor's edge to walk on between a precipice of unnecessary danger on either side."

Definition in a healthy growing and inductive science is a sparse and late-formed product. In early stages prolixity of definition is often a morbid symptom, an imposing substitute for catholic inquiry and well-laid experiment.

Still, if my inexactitude had caused real obscurity, I might indeed regret the neglect of definition; but I never find my critic in doubt as to the meaning I intended to convey. He charges me with using the term Discontinuity in three various senses. I did so. Has this choice of meanings misled Prof. Pearson, or left him in any doubt as to his own course? No: in each of these three senses the conception of Discontinuity is equally odious to him. In each several sense he condemns it as contrary to his experience, a course so logical a critic could not have taken, were he hesitating as to the doctrine upon which his verdict is pronounced. Therefore, though admiring these ten pages of Prof. Pearson's paper as a very elegant display of dialectical skill, I suppose neither of us is in danger of mistake as to their significance in the development of our problem. Were this the moment for play, I would gladly have Prof. Pearson a bout with these same weapons, but now I shall answer in few words.

The three kinds of Discontinuity, though obviously needing dis-

tinct methods of detection and estimation, are *one* phenomenon, in so far as they all illustrate definiteness in variation, existing independently of selection or of "utility."

It is that common property of definiteness or specificity in these variations which fits them rather for study by minute experimental analysis, than for that grosser and less discriminating treatment the professed statisticians have applied. We may consider whether this circumstance has not accentuated the apprehension with which the exclusively statistical school regard this class of fact. It is because simpler methods have already penetrated far below that surface which the instrument of the biometrician explores with such minuteness, that we know that our choice of these simpler methods was right.

In complaining of the lacunae, evidential and logical, to be filled before Discontinuity could stand as a complete theory of evolution, Prof. Pearson mistakes the purpose of my work. My primary engagement was to prepare, not a defence of a special hypothesis, but a catalogue of facts, as a nucleus for further collection. Incidentally I indicated the direction in which those facts pointed. Had my main purpose been merely to show the importance of Discontinuity, a very different choice of evidence would have been made. The work was in many ways imperfect, and is now largely out of date, but it has not wholly failed of its purpose. For one case I should now wish to withdraw as incorrect, the researches of others have contributed many I could now add. No one knows better than I what elements were wanting to prove the views than tentatively advanced: no one better than my opponents which of those elements the lapse of time has supplied.

When the contributions of the biometrical guild are compared with those of the unincorporated group of investigators whom they have lately selected for attack, Mendel, de Vries, F. Ludwig, while the wealth of definition is certainly with the former, few will question that the balance of discovery remains with the latter. It is no little solace to find oneself in such company.

Though unexplored, the fact of Discontinuity was plain enough. The relation of the discontinuous variant, the "mutation" as in certain cases we now say, to its own parents, to their strain, to the rest of the population, was, save in rarest instances, unknown. To have defined these relationships would have been to court certain disaster. Take any aspect of this task. In whatever direction de-

finition had been attempted, it must in those days have been given with reference to *zygotes*, and formulated in terms of their properties. The discoveries associated with the name of Mendel have demonstrated that any such definition must be made primarily with reference to the properties of *gametes*, those of the zygotes being relegated to a subordinate place. These discoveries have provided exactly that "larger and more definite conception of Discontinuity," then only an aspiration. To us the Mendelian revelation has come as the fulfilment of a hope, not as a shattering blow.

How has it been with the biometrical philosophy? Variation, Correlation, fraternal, parental, and so forth, blended inheritance, alternative inheritance and the rest were, as we have been so often told, now at last reduced to definition and could be measured and studied by methods based on those definitions. Where is this panoply of definition now?

One by one, as the divers phenomena of heredity are explored by precise and experimental methods, they are found to manifest various and specific laws. Though intricate, these laws can be detected by minute experiment, and there is as yet no sign that the final determination of such laws is anywhere beyond the reach of orderly analysis. This conclusion appears, not merely from Mendelian cases, but from every set of breeding experiments so far made. For copious illustration it is enough to refer to the *Mutationstheorie* of de Vries. It is not for this region of specific fact that the biometrical definitions were designed; and the naturalist who guides his course by them finds himself utterly at a loss. A pilot might as well try to navigate an archipelago by great circle sailing. Experimental discovery has finally disposed of such projects.

Some estimate of the significance the biometrical school attaches to these discoveries may be gathered from the circumstance that in his recent article on the Inheritance of Shirley Poppies Prof. Pearson has not found himself able even to refer to the Mendelian facts.

In his article on "Variation and Selection" in the new Supplement to the *Encyclopaedia Britannica*, Prof. Weldon follows a similar course; indeed, no other is open to the biometrician. One hint of specific laws in heredity, or of orderly gametic differentiation and regular segregation of characters as a probability, let alone certainty, and the definitions and methods of the biometricians are largely inapplicable.

The case of the colours of Shirley Poppies, one of the subjects—

though hitherto a minor one[1]—of the research named above, shows this at once. The colours are red, pink, white, variously disposed and graded. The problem is to discover the laws of their inheritance. Prof. Pearson's method is to leave the poppies growing together uncovered, letting the insects visit as they may; then to sow the seeds from each mother and observe the inheritance, deducing from these facts the parental and fraternal correlations, etc. Note that in every case the father is unknown. No knowledge of the specific and individual properties of the several varieties was obtained or sought. Crossing, even self-fertilisation, experiments were dispensed with. The result, to speak plainly, is a blur, a confusion, unanalysed, incapable of analysis[2].

Let us consider exactly what this means. It is true no experimental or Mendelian analysis of Shirleys has been made, but there cannot be the smallest doubt that when it is made we shall find that the colours of this species follow laws similar to, if more complex than, those already found in the colours of other flowers—even of certain forms of Papaver (de Vries). To speak more precisely, we shall learn that the colours are not all equivalent, but that each has its own properties in heredity and its own specific behaviour. Some, selfed or fertilised *inter se*, will give nothing but their own type. Some will only be produced by the union of unlike forms, or more strictly of gametes bearing them. In some unions one of the parental forms will disappear partially or entirely, in others a whole series of forms will be produced unlike either parent. There will be resolution of some characters, and doubtless permanent blending or disintegration of others. Each of these processes will have its own statistical expression and follow fairly easily ascertainable laws—which *are* the laws of colour inheritance in the Shirley Poppy.

To such a case the current terms of biometry are plainly inapplicable. The *average* parental correlation, for instance, will be made up of cases where this correlation is always sensibly 0, ·25, ·75, 1, and so on. What that average may be, depends on how many of each

[1] Whether the comments here made would apply also to the main subject of the inquiry, the number of stigmatic bands, we cannot say, but it is by no means unlikely. The work on coat-colour of horses and eye-colour of man is almost certainly invalidated by the same defects. Inasmuch, however, as in these cases the evidence was not obtained by direct experiment, it may be pleaded that the confusion existed before the biometrical studies were begun.

[2] *Biometrika*, II, 1, 1902. In *Nature*, April 9, 1903, a reviewer compliantly declares that this work "marks another long step towards the establishment of a working theory of heredity."

variety took part, how the bees worked them, the comparative ease with which the various forms are capable of fertilising each other—their "prepotency" as it used to be called—and other definite and largely ascertainable factors.

Prof. Pearson makes no reference even to the possibility of differentiation between the several varieties. All are treated alike. We are even told that "In all these cases the actual continuity of the character observed was easy to demonstrate, and there was no hesitation in applying the methods of continuous variation."

The first investigator who makes a study of this case by analytical methods will, I dare predict, find the phenomena full of a beautiful statistical order, which the methods of professed statisticians have only served to obliterate.

It may be urged that the confusion was so complete and the disturbing causes so many or so various, that they may be treated as cancelling, and we can no doubt conceive some proposition to which this method may be applied; but that proposition is not a determination of the laws of inheritance.

I take this illustration of the application of prematurely defined conceptions, because we are told that the work on the poppy colours is in progress and will be largely extended. It may not therefore be useless to ask the observers to make even now a few of those crucial experiments which should precede any such vast undertaking. If Shirleys cannot be had at once in pure strains, then at least let several individuals of each unicolorous form be self-fertilised. In an untried case there cannot be certainty beforehand, but there are known cases so nearly parallel that the result is scarcely doubtful. Now and again, Prof. Pearson alludes to crossing experiments as desirable: he should realise that they form the indispensable beginning.

What would the biometricians say if, in experiments on heredity in poultry, we took away the netting between the pens? Nay—more—if, instead of birds of known origin, we turned down 20 cocks and 100 hens together, some pure, some mongrels of unknown breeds? What should we think of a chemist who proceeded in similar fashion to examine the interaction of unknown substances in unknown proportions? Such a result would, as a contribution to the laws of chemistry, be of equal value with this work on the poppy colours as a contribution to the laws of heredity. If the effort which these thousands of observations have absorbed had been devoted to critical experiment, it must have resulted in useful discoveries.

In all this work the "definitions" of biometry were faithfully followed. Whither they have led their designers we have seen. If the definitions had been left to shape themselves gradually as the diversity of variation and the paradoxes of heredity became familiar by observation, we should have been able to congratulate the biometricians on a very different conclusion. Contemplating these blurred results, I am led to the opinion that Messrs Perrier and Gravier have lately well expressed: "*L'introduction du langage et des méthodes mathématiques dans l'étude des phénomènes biologiques procurent souvent des solutions qui n'offrent que l'apparence de la précision et l'illusion de la simplicité*[1]."

II. *Variation and Differentiation: the elimination of the "too different"*

On the present occasion I can deal no further with those wider issues Prof. Pearson has challenged in defence of his "infant science," and I must return to that comparatively restricted part of the problem regarding which our differences first found expression.

On reading his Memoir[2] and re-reading my first criticism[3], I perceive that some parts of my argument might have been better put. Though I felt the objections strongly, I found them most difficult to express. In what follows I hope to be more successful.

Let me thank my opponent for the labour he has evidently expended in the attainment of lucidity. After reading his admirable exposition of his views, though I may fail properly to express my own, I have no difficulty in understanding his. The painstaking paraphrase of the mathematical argument respecting gametes is particularly welcome, though it illustrates once more how completely the biometrical view of their properties must be reformed in the light of the new facts.

One phrase of mine which has given special offence to Prof. Pearson was used, I need hardly say, without any of that malicious intent he has attributed to it. The passage was as follows:

> Does not then the presence of orderly differentiation in various degrees *compel* us to an analysis of individual instances? In plain language, we shall have to pick and choose our cases, and the value of our coefficient of

[1] *Ann. Sci. Nat. Zool.* XVI, 1902, p. 195.
[2] "On the Principle of Homotyposis, &c." *Phil. Trans.*, 1901, vol. 197.
[3] "Heredity, Differentiation, &c." *Proc. Roy. Soc.*, 1901, vol. 69 [p. 404, *supra*].

homotyposis will depend entirely on how we do it. Has not Professor Pearson himself been so compelled in more than one of his examples, notably that of *Nigella*? Has he any certainty that such an analysis ought not to have been made in other examples also? (p. 414[1]).

The phrase "pick and choose" has seemed to Prof. Pearson indirectly to impeach the probity of his work. No such idea occurred to me; but had I felt such a charge called for, I think I should have had the courage to make it in no doubtful terms. My meaning was, simply, that since *all* cases are confessedly not admissible, choice *must* be exercised, and the problem is, what considerations are to guide that choice?

Prof. Pearson believes that he can provide a test which will keep the wrong cases out and let the right ones in: I incline to the view that such tests are fallacious. The question seemed and still seems to be a fair subject of discussion. My opponent's view may be perfectly natural *a priori*, though I feel no doubt that a fuller experience of the facts will prove it to be erroneous. Let us proceed to debate it.

The objection I have urged to Prof. Pearson's conception that the value of *average* homotyposis has natural significance, arises from the belief that the phenomena of differentiation are such that no fixed and natural line can be drawn between them and the phenomena of variation. In spite of repetition, I regret to find that I failed to make clear that the grounds of this objection are *two*.

For example, I wrote that

in the light of known facts there is serious doubt whether the determination of what Professor Pearson calls the average homotyposis of "undifferentiated like parts" can be attained by his observations, and that there is even graver doubt whether, if it [were] attainable, such a value would have any natural significance (p. 404).

Again:

The reality of the problem as defined by Professor Pearson depends on the assumption that there is an absolute distinction between differentiation and variation among repeated parts, and its solubility depends on the assumption that this distinction can be perceived (p. 411).

Again:

It is not, however, the difficulty of recognition I would now emphasise, but the fact that between the two phenomena no absolute distinction exists in nature (p. 408).

[1] [The paginal references to "Heredity, Differentiation, etc." are to the reprint in this volume, pp. 404–418. Ed.]

In conclusion I repeated:

To state the issue in a word: it appears that the attempt to exclude differentiation by definition must constantly fail in practice and is inadmissible in theory (p. 418).

Surely the contrast between *reality* and *solubility*, *practice* and *theory*, is sufficiently emphatic; but the last passage is quoted by Prof. Pearson with derision thus:

"The attempt to exclude differentiation by definition must constantly fail in practice" (p. 418). That is the "issue in a word" according to Mr Bateson (p. 332, *note*).

My use of the metaphorical term "a word" to include a double idea may be questionable, but I hardly think it justifies Prof. Pearson's partial quotation. To prevent all further ambiguity, let me say that, were I restricted to *one* objection, the one I would and did most insist on is the *theoretical* question of the *reality* of this distinction. There is a good deal to be said on the practical point too, but it is the theoretical objection which has always been overwhelmingly more important to my mind. When therefore Prof. Pearson, on p. 338, states my charge categorically thus:

Differentiation between like organs is not distinguishable,

he omits all reference to the more serious of my objections, namely, the theoretical one, that differentiation is not in essence distinct from variation.

Now in Prof. Pearson's answer this question of a practical distinction is treated; but I have read and re-read that paper without finding any specific allusion to the theoretical aspect. Truly enough he provides a definition of differentiation which he says he can apply. I quite believe that in a great number of cases he could apply it. But the point most interesting is, not whether a definition can be made and applied, but whether it corresponds to some natural boundary between the phenomena. As I wrote:

The practical difficulty he has perceived and in part met, but the more serious theoretical difficulty has, I think, escaped him.

The doubt most prominently before my mind was whether there is a true, natural distinction between variation and differentiation as applied to parts of the same organism. This question I propose to consider first; and subsequently, though the point is of less importance, we will briefly examine the likelihood of a successful application of the distinction in nature, were its validity admitted.

By limiting his consideration to the practical question, Prof. Pearson makes his reply more effective if less cogent. He presents us with the first *Nigella* curve, and the reader shares his contempt for the person supposed incapable of guessing its meaning, or doubtful of the power of mathematics to cope with it. Such an one might be a suitable recipient for any information; so I am scarcely surprised when I am told[1] that the distribution of correlation between the digits of the human hand is such that it is impossible to treat such organs as "homotypes" (*Biometrika*, I, p. 351). May I not protest I knew something of this before?

In my paper five cases were carefully chosen to test *both* the theoretical and practical sides of the conception of differentiation. Each case illustrated a special point. The questions were not all equally easy, and I notice that to three of them—and they not the simplest—Prof. Pearson has not replied at all. The two replies he does make are singularly instructive, as we shall see, and have thrown an entirely new light on the subject of this controversy, but even they refer directly rather to the practical than to the theoretical question.

Though I have thus five times failed to make my meaning clear, I will try once more. Let us take cases most familiar to Prof. Pearson, the Shirley Poppy and *Nigella* capsules. To simplify the discussion let us suppose the character studied to be identical, and call it the "number of segments." In the poppy the range of numbers is considerable, but it was not found that high or low numbers of segments were specially associated with high or low position of the capsule on the plant. In *Nigella*, on the other hand, such an association is obvious, central capsules having on the whole more, laterals fewer segments. Here then there is a clear difference; and if for the moment we defined differentiation as variation associated with position, we should say that *Nigella* showed differentiation, and that the poppy did not.

So far we are agreed. But now let us consider the value and significance of this distinction. *Is the difference between the capsules on the*

[1] Lewenz and Whiteley, edited by K. Pearson. *Biometrika*, I, p. 351. The chief clear deductions from this elaborate "study of the hand" are that the most closely correlated digits are the centrals, III and IV, that I and V are the most irregular, and that proximal phalanges are more correlated than distal ones. It is satisfactory to see that all these conclusions are in excellent agreement with those deduced from earlier studies of meristic variation of digits, namely, that the four fingers are developed about a plane of imperfect symmetry passing between digits III and IV, and that terminal members of meristic series are usually the most variable. (See *Materials*, pp. 79, 358, 405.)

Nigella *in any real way a different kind of difference from that between the capsules on the poppy?* May not the low-number capsule, both in its function and causation, be to the poppy the same as the low-number capsule is to the *Nigella*? *May not the only difference be one of arrangement?* Remember we are concerned to discover whether we can suppose the one phenomenon of variation to be, not merely recognisably, but essentially, so different from the other that the distinction between the two phenomena is not arbitrary but natural.

We might pick the capsules from a poppy and try to arrange them on a model to imitate *Nigella*, the high numbers on the central axes, and the low on the lateral axes. Such an attempt would bring out the fact that the orderly distribution of high and low numbers on *Nigella* is associated with the configuration of the plant, which develops a well-marked central and vertical axis with laterals at various lower levels, while the Shirley on the contrary has the central axis much less emphasised. In it the geometrical relations of laterals to the symmetry of the plant seem to be less definite. On a model constructed like the Shirley, the *Nigella* order could not be reproduced; and to imitate that order we should have to change the configuration of the model. There is, in fact, an association between the more orderly arrangement and the apparently more definite configuration. Why is a variation associated with configuration to be considered a phenomenon essentially distinct from a variation, otherwise identical, not so associated?

From abundant examples we know that even obvious functional[1] differentiation may in some cases clearly be, and in other cases not be, definitely associated with such differences of arrangement. For instance, in the phenomena of gyno-monoecism and gyno-dioecism, the distribution of male, female, and hermaphrodite flowers may be quite irregular to our eyes, or it may be obviously regular. These regularities and irregularities may be presented by different individuals in different degrees, the same species sometimes presenting the one, sometimes the other.

The differentiation in *Nigella* is recognised solely from its association with position, but the association does not *constitute* the

[1] I am interested to see that the biometricians find no difference in the heredity from the meristically different kinds of flowers on the same plant. This is in agreement with the result found by Miss Pertz in the case of *Veronica Buxbaumii*, which she studied with me in 1892–5. (*Proc. Camb. Phil. Soc.*, x, Pt. II, p. 78 [p. 374, *supra*].)

differentiation; in the Shirley poppy the differentiation is masked by the want of such association; statistical methods do not exhibit it, but it need not therefore be non-existent.

We best see Prof. Pearson's conception of differentiation in the passage added (*Homotyposis*, p. 287) to explain this difficulty, where he states that differentiation, "whether due to function, position on the individual, season of production, etc., is usually connected with one or two well-marked dominating factors," and so "is statistically discoverable[1]." In his latest paper the allusion to differentiation as being "due" to position, or "due" to age, is frequent and even more explicit[2]. How can differentiation be "due" to function, or "due" to position? How shall we tell which is cause and which consequence? There may be *association*, or, as Prof. Pearson says, correlation, between differentiation and position, but why cannot the differentiation exist without this association of correlation with position? May not there be *no* well-marked dominating factor that, by its association with the difference we are considering, will proclaim it a differentiation rather than a variation?

On the Metropolitan Railway I believe the trains are generally arranged with the first-class carriages in the middle and the seconds and thirds at each end respectively. On other railways the arrangement is apparently irregular: would Prof. Pearson maintain that on these other lines the differentiation between the classes is less complete?

So far as I can see, as applied to parts of one individual, *differentiation* means a considerable or frequently observed difference that we look upon as phylogenetically permanent and orderly, and *variation* a less considerable difference that we look upon as impermanent and irregular; but nothing more precise. These are the senses in which I use the words, and I believe the want of precision lies not in me but in nature. The attempt to detect the distinction by a precise statistical method adds only an appearance of precision.

It is consolatory to me to find that, though treating my objections with superior scorn, Prof. Pearson has not selected my problem of the frog's corpuscles for an answer. I took this case for two reasons. (i) It is a case to which he says homotyposis can be applied. (ii) We have good reason to believe that differentiation—in any

[1] If it were declared that "differentiation is statistically discoverable" and that the term is used in that application, this declaration would verge on *petitio principii*.

[2] *Proc. R. Soc.*, 1903, LXXI, pp. 288 and 313.

acceptation—exists between corpuscles[1]. No stretch of imagination is needed to conceive various individuals of the same species presenting such differentiation in various degrees of expression. Some may even, as I put it, have a class of corpuscles absent in others, though the individuals possessing them may be connected with the individuals not possessing them by several grades. Nevertheless we have, so far as I know, no criterion, theoretical even, not to say practical, for distinguishing such differentiation from the normal variations which are to give us the measures of homotyposis. This objection is surely not "idle," as Prof. Pearson reiterates. In asking this question of the corpuscles, I had a definite and analogous problem in view. In my own work I am concerned with the differentiation of germ-cells, and I had a curiosity to know how in such a case, where position does not so far help us, Prof. Pearson would distinguish between differentiation and variation. I am sorry he has not assisted me in this matter.

I suggest, then, that there is no strict or *natural* distinction between *variations which are to be included* in calculating average homotyposis, and *differentiations which are to be excluded*. The latter are more orderly or considerable variations, the admission of which will lower the homotypic value.

But, apart from the question of a natural distinction, there is a very serious practical difficulty too. Assume that we are entitled to draw a theoretical line between variation and differentiation, how shall we recognise it? As I wrote, differentiation is a "subtle and evasive quality." We have only to turn to the remarks and notes on the several cases investigated to witness the perpetual trepidation both Prof. Pearson and his assistants were in regarding this difficulty. Read Miss Fry's note (*Memoir*, p. 304) respecting her difficulties in collecting holly leaves. Which were to be taken, which left? On this Prof. Pearson remarks:

> It will be seen that in this point, as in others, much had to be left to the judgment of a careful observer.

A friend has acutely remarked to me that Homotyposis seems to be concerned "with things that are different, but not *too* different," and I fancy a great deal of the collecting had to be done with this principle in view. It is indeed the only principle which could be consistently applied.

[1] Cf. Sherrington, *Sci. Prog.*, II, 1895, p. 415, where a good general account of these phenomena is given.

It has been to me a matter of no little surprise that Prof. Pearson has thought the production of the *Nigella* diagram a sufficient answer even to this practical question. As it happens, the statistics expose the differentiation. In the best strains I can scarcely imagine a good observer drawing the plants from memory, without indicating it in some degree. But even in *Nigella*, were it not for the effect of the two *Fibonacci* maxima on 5 and 8, corresponding to the laterals and centrals respectively, Prof. Pearson's statistics need not have suggested differentiation. The numbers might in any such case present a homogeneous chance distribution, and unless the association of low numbers with laterals had been recognised by ordinary observation, statistics based on indiscriminate collection would not then reveal the differentiation. This very mistake was made in the case of the beech leaves, because the collecting was done without an attempt to distinguish by observation whether there was any differentiation according to serial position on the shoots[1]. Similarly, in the *Equisetum* whorls (*P.R.S.* LXXI, p. 305), it is not the statistics *alone* which prove the differentiation, but the grouping of the statistics according to

[1] In a general argument I am loth to introduce objections *de facto*, or to plead that any special case was vitiated for a special reason. But since this paper was written I have received the valuable memoir by T. Tammes, which contains evidence of so direct a character that it seems to call for some notice. This work showed, amongst other things, that the case of the number of veins in the leaves of the beech is beset by this very difficulty, though apparently one of the least dubious of Prof. Pearson's homotypes. It was found, as might be expected, that the number of veins is low in the lower leaves of an annual shoot, increases in the middle leaves of the shoot, reaching a fairly definite maximum, and decreases in the leaves placed higher up on the shoot. There is certainly an "effect comparable with the errors of random sampling." The leaves of the middle are in fact like the central capsule of *Nigella*. The whole range, the maximum, and the position of the maximum, and the number of leaves exhibiting it on the same shoot, will of course differ on different parts of the tree, on different trees, and different varieties; but the fact that the "variation" in number of veins might with equal propriety be called "differentiation" is obvious. (See T. Tammes, *Die Periodicität morphologischer Erscheinungen bei den Pflanzen*, Verh. K. Wet. Amsterdam, Sect. II, IX, No. 5, 1903, pp. 80 and 83.) Prof. Pearson found the homotypic correlation in this case ·57. This means that he picked leaves neither too different nor too like, or about equivalent quantities of each. Another collector might as easily have picked leaves giving about ·4 or ·7.

There is no suggestion of the indefiniteness of arrangement supposed to characterise the variations of homotypes. The distribution of the differentiation varies of course on individual trees and varieties. Yet, so far, in all beeches I have looked at, the *lowest* leaf of each annual shoot is so obviously differentiated that I suppose all observant collectors would exclude it. The *top* leaf might be included by some, and excluded by others. Will some student of homotyposis indicate the leaf at which the series of pure homotypes begins? Having decided this for the beech, will he then try the elm?

position of the whorls on the stem. The case of the poppy capsules is merely one where we have not as yet discovered any factor according to which we can group the statistics as a preliminary to testing for differentiation.

This practical difficulty is one I would gladly demonstrate by numerous illustrations even from Prof. Pearson's Memoir, but I scarcely think that necessary, and I fear also to divert attention from the incomparably more important theoretical aspect of the problem. I would, indeed, waive the practical difficulty altogether if such a course would make the natural difficulty more intelligible.

III. *Variation and Correlation: the elimination of the "too like"*

Homotyposis is concerned with things "which are different but not *too* different"; but conversely it contemplates things which are like but not *too* like. By the introduction of either the *too different* or the *too like*, the significance of the average is jeopardised. The introduction of the former will lower the homotypic correlation, the latter will raise it. If both are successfully eliminated, or admitted impartially, a clustering round the mean value will no longer surprise us. I have dealt with the "too different," I will now speak of the "too like."

We have seen how Prof. Pearson hopes to exclude the "too different": this answer could be foreseen. It was, however, with a genuine astonishment that I read his reply on the second point. My former criticism did not deal with this difficulty explicitly. It had not been alluded to in Prof. Pearson's Memoir, though it could hardly be supposed to have been overlooked. But to test this question of the "too like" I presented a special problem which has had the good fortune to be dealt with in his reply. My question was put in the following form:

> Yet another and even clearer illustration. The two claws of a Crab are a pair of homotypes. Their homotypic correlation in respect of any character, length for example, might be determined. Now there are species of Crab in which the two claws are approximately equal or undifferentiated. On the contrary, in some species the right, in others the left, in others the right or left with varying frequency[1], is differentiated in size and other characters. Can it be decided in such a case which deviations from, or

[1] A valuable study of this phenomenon in *Gelasimus* has since been published by Yerkes, *Proc. Am. Ac.*, XXXVI, 1901, p. 417.

approaches to, bilateral symmetry are, *as variations*, to be included in a determination of homotypic correlation, and which are to be rejected as due to changes in differentiation?

In further explanation I added the following passage:

The diversity due to differentiation may exhibit a "homogeneous chance distribution," as for example, in my illustration of the Crab's claws. We have only to suppose that the "mode" of the population falls on a form with claws approximately equal, and—to take the simplest case—that the frequency of both right-handed and left-handed differentiation is inversely proportional to the magnitude of the differentiation, a state of things common enough in nature.

Prof. Pearson's reply is of extraordinary value, and must, I think, go far towards elucidating his conception. He says he is well acquainted with phenomena of this class and never thought of including them. Had he done so they would have brought up "the homotypic average to somewhere between ·9 and 1!" No doubt: how then does he exclude them? He writes:

The correlation between right and left member is, in my sense of the word, *organic* and not *homotypic*. I term the correlation between two members "organic[1]" when its value is wholly or partly determined by the fact that, for the welfare of the individual, the members must within certain limits "fit," they have a function to perform in common and their mutual relationship has been controlled during its evolutionary development by the existence of this common end.

Can these be the words of the logician who reproached me with

[1] It seems strange that the form of the definition of "organic correlation" here given should differ so widely from that provided in the original Memoir. The matter may have no importance, but as Prof. Pearson is particular in definition he may wish to clear it up. In *Homotyposis* (p. 294) we read the following definitions with others:

"I shall call undifferentiated like organs *homotypes*, indicating that they are types produced by the same mould or individual. Thus two leaves of the same tree, or two blood-corpuscles from the same frog are *homotypes*; their resemblance will be homotypic, and the character by which their resemblance is quantitatively measured will be the *homotypic* character. I shall speak of *homotypic* correlation and distinguish it from *organic* correlation—although, of course, the former is in a sense organic. *By organic correlation I refer to the correlation between two different characters in the same organ* [my italics]; by homotypic correlation to the correlation between the same or different characters in a pair of homotypes." As far as I can judge, this definition of "organic correlation" bears only remotely on the idea introduced under the same name in the present text. In the Memoir, however, the term is used as there defined, especially for the relation between length and breadth of the same organ. The conception of "fit" for "welfare" seems to be a later development, and I cannot find an explicit reference to it in the Memoir.

"*Idola fori*[1]," and who warned me not to "pour the child away with the bath"? Do these appeals to the need for "fit," to "the welfare of the individual," to "control during evolutionary development by the existence of this common end"—*not merely as fancies, but as recognisable factors*—come with force from one who bade us employ only conceptions based on numerical evidence? *Idola fori!* Are they truly more dangerous than *Idola specus*? If fancies we must have—and I hope they will not cease in my time—let them at least be public, daylight fancies, simile and illustration, images confessed: rather than those private and wonder-working phantasies of the Cave; which, though their superstitions were long ago outwardly forsworn, still distort and rule the judgment.

Mutual relationship controlled by the existence of a common end! Truly Prof. Pearson has assumed an "onerous cause": must he not encounter "Occam's razor[2]"? Let a brother-biometrician rebuke him. In the new *Encyclopaedia Britannica* (s.v. *Variation and Selection*), Prof. Weldon, with more prudence, declares that "a fertile source of misconception has hitherto been the habit of testing the theory of natural selection by our power of imagining an obvious use for the characters of animals which undoubtedly survive; and the validity of the theory has been largely made a question of our power to recognise the 'adaptive' or 'useful' nature of specific characters. In our present condition of ignorance concerning the function of any organ in the great majority of animals, it is evident that our theories of their utility must often be erroneous or imperfect: the only really adequate test of such theories is the statistical test" [of change in death-rate or fertility].

But if Prof. Pearson defends by interposing "welfare," our next move discovers a check that must surely be fatal. We are about to exclude the "too like," on the ground that their correlation is "organic," and that "its value is wholly or partly determined by the fact that, for the welfare of the individual, the members must within certain limits 'fit.'" Since there are species of crabs in which the claw of *one* side, say the right, is differentiated, being for example larger,

[1] Prof. Pearson's reproach "*Idola fori*" was called forth by my suggestion that the terminology in use for organic repetition of parts might be assisted by ready metaphors taken from the phenomena of rhythmical vibration. This would be merely to extend our present practice. Will he state in what sciences he first became familiar with the phenomenon of "segmentation," and whether in his later studies he has felt scruples as to the use of such *Idola fori* as "segment," "node," or "internode"?

[2] See *Grammar of Science*, ed. 1900, pp. 92, 377, 512, 536–7.

with some regularity, we may therefore say that the value of the correlation between the two claws in such species has been "wholly or partly determined by the fact that, for the welfare of the individual, the members must within certain limits 'fit'" by *not* fitting. Why, then, may we not, proceeding to the case of *Gelasimus*, where "rights" and "lefts" are about equally frequent, say that the "welfare" of half the population has decreed that their claws shall "fit," by not fitting in one way, and that the "welfare" of the other half of the population has happened to be reciprocal?

Positively, if we can exclude the "too like" by the test of "welfare," we might have excluded the "too different" by the same test, and have demolished both our difficulties by one well-aimed postulate, thus: *Parts are not homotypes if their correlations affect the "welfare" of the individual.* It was because I foresaw some of these possibilities that I declared the crab's claws were an "even clearer illustration"—not "of homotyposis," which my opponent represents me as saying[1]—but of the unreality of the conception.

The biometricians have so far produced no criterion of whether a part is or is not in "organic correlation" with another part, other than the magnitude of the correlation itself, and their personal estimate of "welfare" or "fit." It will next be seen that even these two considerations are interdependent.

This is well illustrated by the following passage, where they compare the very *high* correlation found between the two hands, and between the parts of one hand, with the *low* correlation between the bony parts of the skull[2].

> The hand is a most highly correlated mechanism, and given one long bone of one digit, the range of variation occurring in any other long bones of the same or the other hand is wonderfully small. *It is hard to hold any other view than that this degree of fitting is the result of selection for physical use.* [My italics.]
>
> ...We should expect sensory and mental fitness to depend upon high degrees of correlation between the parts of the sensory and mental organs. But it still remains a noteworthy fact that the bony parts of the skull are on the average not correlated with even a third of the correlation of the parts of the hand, and this fact alone seems to account for the small apparent relationship between intellectual ability and measurements on

[1] *Fundamental Conceptions*, p. 342.

[2] Lewenz and Whiteley, "A Study of the Hand, etc." Ed. K. Pearson. *Biometrika*, I, p. 346.

the head. We should expect to find the parts of the organism on which intellectual efficiency depends highly correlated like the parts of the hand on which physical efficiency depends; the absence of high correlation in the parts of the skull suggests that it is not chiefly upon its case that brain efficiency turns.

Stripped of irrelevancy, the argument may be put in syllogistic form, thus[1]:

> *High correlation is due to the need for "fit":*
> *Correlation due to the need for "fit" is not homotypic:*
> Therefore, *High correlation is not homotypic.*

Why are we compelled to treat high correlation as a product of urgent or prolonged selection, or to regard it as anything but an incident of, or corollary from, the mechanical conditions of cell-division and growth[2]?

In further explanation of the properties of "organic correlation" Prof. Pearson continues:

> In homotyposis this purpose, *i.e.*, the performance of a common function as controlling the relationship, has either no existence or is insensible—the mutual relationship is due to the individuality of the producer, and is practically uncontrolled by the importance to the individual of the homotypes performing at some time related but really differentiated parts in a common function. It is not vitally important to a beech-tree that one leaf having 12 veins upon it another gathered from anywhere else on the tree should also have 12 or nearly 12. But it is important to a man that if he has one femur of 456 mm. the other femur should be within a few millimetres of the same length.

May we hope to read in *Biometrika* the statistical proof of this fact about the beech-tree or was it discovered by natural acumen?

But though Prof. Pearson is so well informed about the beech-tree, has he ever watched how a beech-tree grows? He may, if he so desire, assume that the assimilation and respiration need not be seriously affected in connection with a change in the veining, but how about

[1] On p. 326, Prof. Pearson does not altogether avoid this very *circulus in probando* in treating the converse difficulty of differentiation. Commenting on recognised differentiation in the Woodruff, he states that "The great reduction in the correlation, the value of which is only ·1733, shows how unsuited the material was for the purposes of the present investigation." But if the correlation-value *itself* measures the suitability of the material, labour would be saved by excluding high and low correlation by original definition. The mean value ·5 would thus be reached with the utmost certainty.

[2] A discussion of this subject will be found in *Materials*, pp. 76, 568, etc.

the cell-divisions? Quantitative proof apart, I should have imagined that the departure from the normal coordination of the planes and rhythm of cell-division, resulting in a change in the number of veins, appropriate to a given leaf of a given tree[1], would constitute a departure from the normal physiology at least as significant to the viability of a beech-tree as a change in length of leg to a man. The leaves are not stuck on from without, like the candles on a Christmas-tree, but arise by most complex and coordinated processes of division.

If Prof. Pearson were presented with a pair of opposite leaves of a honeysuckle or a pink, he would doubtless declare that the closeness of their correlation was due to the need for "fit" and that it was therefore "organic." Could he maintain that there was more "organic" correlation between them than between two adjacent, but alternate, leaves of a beech?

If we conceive a beech affected by a variation consisting in a departure from the normal succession of vein-numbers in passing from leaf to leaf, the configuration of at least the shoots affected, and probably of the whole tree, would be profoundly changed. We might possibly record such a specimen as a notable mutation. If anyone doubts this proposition let him pick the leaves off an expanding shoot of a beech and rearrange them, interchanging leaves with different numbers of veins. The result is chaos. Such a variation could only be achieved by innumerable readjustments and fresh coordinations, beginning perhaps from the first cell-division of the zygote. Imagine the hand of a man with the index and medius transposed, and the comparison gives a scarcely exaggerated picture of the aberration involved by transposition of a 14-veined with a 16-veined leaf on the beech shoot. Nevertheless Prof. Pearson supposes interchangeability to be a property of homotypes. For in dealing with the crab's claws he remarks that, "in right and left-hand members we have a differentiation in function, one member could not possibly replace the other," and that, "such cases are very fully excluded by the definition of homotypes." This reference to interchangeability as a test of homotypes raises some entirely new and instructive points. In gathering the beech or holly leaves for homotyposis, was an attempt made to see that the leaves chosen *were* interchangeable? A close analysis would soon reveal that the leaves of a tree are, in several distinct ways, scarcely more interchangeable than the claws of a crab. I greatly

[1] See p. 432.

regret that Prof. Pearson offered no solution to my problem of the population of radiate organisms, of which some showed indications of bilateral symmetry, while others were irregular. An examination of this case would have immediately shown that organs repeated in radial symmetry are almost the only parts to which the conception of interchangeability can be even loosely applied with propriety.

Respecting the crabs, I did not ask, as he supposes, how he would recognise *established* differentiation, which I could do myself in an old-fashioned way, but a more serious question. Starting from a state of approximate equality between the claws, combined with variability so slight that none of us would wish to call it differentiation, we should reach stages of greater variability in which, if we were presented with an extreme specimen, whether right or left-handed, we might at once call the condition in that specimen differentiation. If Prof. Pearson puts in the specimens or populations with equal claws, he raises his average unduly; if he puts in the specimens or populations presenting differentiation, he lowers the average unduly. It may be urged that these two sources of error will sometimes cancel each other. This however is only true of special cases. Moreover, every appeal to such cancelling diminishes the significance of that clustering round ·5, the average of all possible values, which Prof. Pearson considers characteristic of homotypic correlation. Where will he draw the line in *theory* and *practice*, by a statistical method?

Now I protest that this question is neither "idle" nor "captious." The case is typical of innumerable phenomena of repetition of parts we daily encounter, and unless it can be dealt with, the whole fabric of homotyposis becomes a figment.

These considerations apply to linear as well as to bilateral repetitions, as Prof. Pearson himself perceives. His answer to my case of the Syllid proves this.

"Suppose," I wrote, "that in a polychaet, say a Syllid, there is marked differentiation between segments at the anterior and posterior ends separated by hundreds of segments apparently undifferentiated, bearing appendages similarly undifferentiated. We may determine the homotypic correlation of these appendages. So long as differentiation regularly and conspicuously begins at a certain region we can exclude it. But suppose in some individuals it begins at one segment and in another at another, as it almost certainly would do, how should we know which specimens or which segments must be rejected as introducing a confusion through

differentiation, and which must be included in reckoning homotypic variation? If differentiation is irregular, will it not change the apparent homotypic correlation?"

Prof. Pearson provides an answer, not wanting in vigour, but it is not an answer to my question, which I take leave to repeat. He says:

> Mr Bateson takes the case of a syllid with numerous segments apparently undifferentiated but with marked differentiation of the segments at the posterior and anterior ends. How, he asks, are we to consider which, if any, of these segments are suitable for investigating homotyposis?

The reader will perceive that this question is much simpler than mine (which has nothing to do with "suitability"), and Prof. Pearson easily disposes of it by reference to ordinary methods of statistics. But my point, of course, is that the homotyposis of some of those individuals and some of those segments *must* be included as undifferentiated, and some *must* be excluded as differentiated, and that the slightest acquaintance with nature familiarises the naturalist with series connecting the two classes—I may almost say wherever the phenomenon of repetition of parts is met.

The problem of the Syllid worm is that of the beech-tree by another name. The long body is the branch; the appendages are the leaves; some of them are differentiated more, others less. In some individuals the differentiation becomes noticeable at one segment, in others at another. Prof. Pearson feels happy in his study of the beech leaves, but unless I greatly mistake he was not without misgiving on this matter of the Syllid; for he says

> Probably I should not take such a case for studying homotyposis at all, for each segment may bear an *organic* relation to its neighbours; there may well be a condition—as of fitting of adjacent parts—which is expressly excluded in the production of pure homotypes.

But where shall we seek for examples of repeated parts, homotypes, leaves, leaflets, fronds, segments, where this consideration of "fitting" is excluded by *nature*, as well as by definition? Has Prof. Pearson ever dissected an apical bud of the beech, the holly, the chestnut, or the ash? When he does, he may feel less easy as to the limitations of "fit," and as to the propriety of a distinction between "organic" and "homotypic" correlations.

How he has so far failed to feel this difficulty I am at a loss to comprehend. For his very word "homotypes" was as we were told (see note, p. 434) made to denote that they were "types produced by

the same mould." I note with interest that though in the original Memoir a good deal was said as to the difficulty of excluding differentiation, no special reference was made to the "fit" difficulty. But in the last addition[1] to the subject by Prof. Pearson I find these words:

> The subject of differentiation due either to position or age[2] is, of course, a difficult one, but it does not seem at all beyond biometric treatment. The greatest difficulty which it seems to me will have to be encountered is not that of discovering and allowing for differentiation due to serial position, but in ensuring that when this has been allowed for, there is not remaining an organic correlation due to the necessity of adjacent parts "fitting."

As this "greatest difficulty" was not alluded to in the first Memoir, though other difficulties were, we must suppose that Prof. Pearson has already discovered some unexpected developments in his problem, and I am sanguine that if he will follow the same train of thought which led him to the difficulty about "fit," it will not be long before the "idleness" of my objections will be less manifest than at first. In concluding this section of my argument I therefore repeat that so far as appears at present it is not evident that Prof. Pearson has any criterion other than personal judgment which will guide him in the exclusion, either of the "too different" or of the "too like" from his calculation of average homotyposis; and consequently, that average value has "no more natural significance than would the average variability of all organisms measured by their 'Standard Deviation' from their various means, or the average size of living cells, or the average weight of all ponderable bodies."

IV. *Repeated Parts and Brethren*

In my paper *Heredity, Differentiation*, etc., I pointed out that Prof. Pearson's parallel between the homotyposis of "undifferentiated like parts" and the correlation between brothers was wrong in form. If a comparison is to be instituted it should be made with the correlation between *undifferentiated like* brothers. If the differentiated and the unlike are excluded in the one case, they should be in the other. I am answered as follows:

> My reply is that I was dealing with types of life in which differentiation between pairs of brothers is not sensible, and therefore I was perfectly

[1] *Proc. Roy. Soc.*, LXXI, p. 313.

[2] On an earlier page I have protested against this misuse of the conceptions of cause and effect. With equal propriety we might speak of the position, if not the age, as being "due" to differentiation.

justified in seeking the correlation of undifferentiated like organs, my homotypes.

But this is merely an answer on the point of fact, and it scarcely does justice to my objection, which was primarily on a point of form, and seemed likely to appeal to one interested in such matters. As a practical answer it is—with a serious qualification to be soon considered—sound enough. I have often felt it is an unfortunate characteristic of the biometricians that they do, as a rule, deal only with types or features which show, or are declared to show, no differentiant variation between brethren. In my own studies, differentiation between brethren plays so large a part, that it seemed strange to find no reference to the existence of the phenomenon in the formulation of Prof. Pearson's parallel. It was therefore in order to emphasise the need for wider conceptions, and observations of variations of many classes, that notice was called to the formal point. If Prof. Pearson will follow out the thought I thus ventured with due circumspection to suggest to him, he will find it lead to the discovery that if we *may* compare brothers with parts, then differentiant or discontinuous variation between brethren closely corresponds with differentiation between the parts of an organism. The latter phenomenon he is familiar with, and the fact may aid him to reconcile himself to differentiant variation between brethren also.

In the case of the correlation between brethren we shall also meet that difficulty respecting the "too like" which we have already found in the case of parts. Of this I said nothing in my first statement of objection, because, though differentiated parts had been excluded, we had had no explicit declaration that highly correlated parts were to be excluded also. But as there is differentiation between brethren, so there may be a very close correlation between them.

In reckoning average fraternal correlation, Prof. Pearson brings to account the correlation calculated by a special, and I suspect illegitimate method, in the case of coat colour of horses and dogs, but why is not the fraternal correlation seen, say, in the colours of pure races included? In any pure race such correlation is sensibly perfect, and we should have thus to include many cases, which like the crab's claws, would tend to bring the average up to about ·9 or 1. The same argument holds in the case of racial characters in general. In Prof. Pearson's parallel the correlation between brethren is named without any qualification, but he must clearly be understood to refer to those

brethren that are neither "too different" nor "too like." The parallel can only be correctly instituted between, on the one hand, parts which are both undifferentiated and have no such close correlation between them as to be sensibly identical; and on the other hand, brethren which neither exhibit differentiant variations, nor such close correlation as to be sensibly identical. As soon as this is done, the interrelationship of the various phenomena is clear. The comparison may be represented in tabular form thus, comparables in respect of any given character being placed under *A* and *B*:

	A	*B*
Parts presenting,	sensibly complete correlation or identity.	differentiations.
Brethren presenting,	sensibly complete correlation or identity.	specific or differentiant variations.

Between the highly correlated *A* group, the "too like," and the differentiated *B* group, the "too different," there is of course a mass unanalysed, but not therefore beyond the reach of analysis. It is difficult to conceive how the *average* correlation of that mass, whether homotypic or fraternal, can be far from ·5; and no importance can be attached to the truistical observation that the correlations of parts or brethren included in it approach that value.

If Prof. Pearson's parallel had been correct in form, and had excluded differentiation, not only between *parts* but also between *brethren*, I think he might have been led on to surmise why it is that the average value for the correlation he calls Homotyposis agrees so nearly with the average value he has determined for the correlation between brethren. In both cases he is merely measuring normal fluctuations, controlled by unanalysed and apparently "indefinitely numerous" causes, not because other classes of variations do not occur, but because the conspicuously differentiant have been excluded, and others *probably* of the same nature have been treated in such a way that the evidence of differentiation is obliterated. In collecting the material for homotyposis the "too different" have been excluded as differentiated: in estimating the correlation between brothers he has seldom been confronted with an indisputable case of "differentiant" variation, owing to his choice of subjects, and his method of treating them. The need for its exclusion has thus been less apparent. To this there is one notable class of exceptions, those in which *colour* is the character considered, whether of the coats of horses

and dogs, or of the human iris. Though in these cases something like real, differentiant or specific, variation between brethren may be surmised to exist, the materials provided by the biometricians do not clearly exhibit it, or give it proper weight. With such an illustration as that of the Shirley Poppy (see p. 423) before my eyes, I do not feel certain that the material has been handled by the investigators in such a way as to bring out the differentiation if there were any. I notice Prof. Pearson explicitly says that his methods can only be applied to the coat colour problem on the condition that, "The characters should admit of a quantitative order."

I find it impossible to suppose that the coat colours of horses, for example, admit of such an order, a subject I may hereafter treat more fully[1].

Such observational indications as we have of the nature of pigmentation, and experimental knowledge of the physiology of its heredity, dispose me to doubt the validity of the methods by which correlation has been biometrically measured in these cases, and until careful experimental tests have been made, I incline to the view that we have here examples of those "blurred" correlations which we suspect more definitely in the Shirley Poppies.

As soon as the comparables are properly grouped (see p. 443) the significance of the reference to the phenomenon of geometrical symmetry in cell-division becomes evident. Prof. Pearson regards the sensibly identical parts (under *A*), as having acquired their high correlation by a long process of natural selection. But having regard to the apparently indiscriminate occurrence of such identity or symmetry, as much in seemingly trifling structures as in those for whose correlation we can suggest a use, I prefer for the present to accept such identity as an incident of the mechanical processes of division. Similarly the sensibly identical brethren must be regarded as the result of symmetrical divisions whether of gametes or zygotes, the

[1] If the colours of horses are to be arranged in a quantitative order at all, not one but several series are required. We are concerned with the quantitative variations of *at least two* sets (probably more) of pigments, the blacks and the yellows. Next we have to consider the ways in which they may occur in combination with each other, or with white. Why is a chestnut horse physiologically nearer to a white horse than a black is? Why is bay or brown quantitatively intermediate between black and chestnut? Pending breeding experiments of an elaborate character beginning from pure races, the specific behaviours of the several colour types cannot be determined. The stud-book descriptions are far too slight to justify deductions of this kind. The colours of the mane, tail, the "blaze," etc. must all be considered before the specific laws of colour-inheritance in the horse can be traced.

most striking case being that of homologous twins. Conversely under *B*, we compare parts and brethren, which arise from each other respectively by differentiant divisions whether of zygotes or gametes.

In conclusion, as I would not willingly engage in a purely negative cause, let me offer a positive suggestion.

We recognise symmetry of division as characteristic of the mode of origin both of the like parts and of the like brethren. We know further that the divers tissues of the body arise from a single cell, the fertilised ovum. Now, if there is a true parallel between the differentiated parts and the differentiated brethren, may not this parallel perhaps extend to the histological processes by which both arise? We do not yet know at which of the gameto-genetic divisions segregation of characters takes place, but the discovery may be made any day. It seems to me not impossible that a hint of the nature of those differentiant or segregating divisions may be found by a study of some of the more accessible and recognisable differentiant divisions by which the tissues arise in the body. There are in animals and plants several cases where the germ of one organ arises by a definite differentiant division from a single cell or group of cells, and I am not without hope that the study of the minute histology of such divisions may give an indication as to the nature of the differentiant divisions in gameto-genesis also. To the unravelling of these conceptions there is as yet but one clue, which, if Prof. Pearson will pardon me, I will name once more, *Symmetry*.

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